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From tropical shelters to temperate defaunation: the relationship between agricultural transition stage and the distribution of threatened mammals

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Abstract

Aim

Agriculture is a key threat to biodiversity, however its relationship with biodiversity patterns is understudied. Here, we evaluate how the extent, intensity, and history of croplands relate to the global distribution of threatened mammals. We propose two hypotheses to explain these relationships: *shelter,* which predicts that threatened species concentrate in areas with low human land use; and *threat*, according to which threatened species should concentrate in areas of high human land use.

Location

Global.

Time period

c.B.C.6000 - 2014.

Major taxa studied

Terrestrial mammals.

Methods

We used boosted regression trees (BRT) that include spatial autocorrelation to investigate the relationship between the proportion of threatened terrestrial mammals (as defined by the IUCN Red List) and multiple metrics describing agricultural extent, intensity and history derived from remote sensing data and statistical projections. Data were analysed with a grain size of ~110 x 110 km at both global and biogeographic-realm scales.

Results

Agricultural extent and intensity were the most relevant indicator types, with specific metrics important for each realm. Forest cover (extent) was identified as important in several regions. Tropical regions in early agricultural transition stages (e.g., frontier landscapes) were consistent with the *shelter* hypothesis, whereas patterns found for regions in later stages (e.g., intensified agricultural landscapes) were mostly found in temperate regions and agreed with the *threat* hypothesis.

Main conclusions

These results highlight the need to consider multiple land-use indicators when addressing threats to biodiversity and to separately assess areas with divergent human and ecological histories in global-scale studies. Different relationships associated with different agricultural transition stages suggest that high concentrations of threatened species may have contrasting meanings in different regions worldwide. We propose a new unifying hypothesis following a cyclic relationship along agricultural transition stages resulting in alternating negative and positive relationships between agriculture and threatened species richness.

Introduction

The demand for agricultural resources (food, fodder, fibre, and bioenergy) is expected to increase rapidly due to human population growth and the rise in per-capita consumption (Kastner *et al.*, 2012; UN, 2014). From the current 38% of land surface allocated to agriculture (~68% pastures and meadows, ~31% arable lands and permanent crops; FAOSTAT, 2011), projections predict a 10-25% increase (from 2005 levels) in global cropland extent by 2050 (Schmitz *et al.*, 2014), primarily in highly biodiverse areas of South America and sub-Saharan Africa. Simultaneously, further intensification is expected to occur in many developing regions (Dietrich *et al.*, 2012).

Agriculture is one of the main threats to terrestrial biodiversity (Salafsky et al., 2008; González-Suárez et al., 2013; Böhm et al., 2016). The effects of agricultural expansion and intensification on biodiversity are varied and difficult to differentiate because both processes often occur simultaneously. Studies have shown that biodiversity decreases as agriculture expands into natural areas (e.g. Kerr & Deguise, 2004; Koh & Wilcove, 2008), mainly by means of habitat loss and fragmentation (Gasparri & Grau, 2009). However, some impacts on biodiversity may be detected only years later yet have significant consequences, such as the destabilization of ecological interactions and the establishment of non-native species (Kuussaari *et al.*, 2009; Vilà *et al.*, 2011; Fontúrbel *et al.*, 2015). In addition, increased intensification of existing agricultural land negatively affects species via habitat degradation (e.g. the addition of more chemicals increases pollution), by reducing geographical ranges (e.g. species may persist within extensive croplands, but not in intensively used ones), or by disrupting community composition (Flynn et al., 2009; Kleijn et al., 2009). Given the potential for further expansion and intensification of croplands, understanding how biodiversity is distributed relative to different agricultural practices is crucial to safeguard remaining biodiversity.

Agricultural land use indicators can be classified into metrics of extent and intensity. When assessing the patterns and impacts of land use and biodiversity at the global scale, few studies assess both the extent and intensity of use (but see Phalan *et al.*, 2014; Kehoe *et al.*, 2015, 2016, 2017; Shackelford *et al.*, 2015). There is also a temporal dimension that might be key to interpret the distribution of current extinction risk (Ellis *et al.*, 2013; Faurby & Svenning, 2015), but it is often overlooked. Past modifications in biotic and abiotic conditions caused by agriculture may have long-lasting indirect and lagged effects on ecosystems, which may continue even after agricultural uses cease (Foster *et al.*, 2003). Besides, areas with a history of profound land use might have already lost the most sensitive species and/or show sub-optimal habitat conditions. Conversely, where less intensive land uses have prevailed over longer time periods, species may have adapted to or even become dependent on low-intensity human land uses (Walker *et al.*, 2004). This difference in observed vulnerability mediated by past human pressures can be seen as a form of extinction filter (Balmford, 1996). Biodiversity is inherently complex and cannot be reduced to one number, given the impracticability of assessing all components of biodiversity (genes, species, ecosystems, functionality, etc) and the difficulty of designing a valid metric for all species (Magurran, 2004; Santini *et al.*, 2016). When exploring human threats, it seems reasonable to use a metric that incorporates knowledge on the conservation status of species. Threatened species' richness is one of the metrics used to establish conservation priorities or biodiversity hotspots (e.g. Brooks et al., 2006; Grenyer et al., 2006). In these cases, preserving the maximum number of threatened species is a target in and of itself. High threatened species richness can also serve as a warning signal of higher concentrations of threatening activities.

Understanding which metrics of agricultural land-use change may best predict threatened species distribution is useful in interpreting global patterns of threatened biodiversity. Here, we evaluate multiple land use metrics under the framework of two hypothesized relationships. The first hypothesis (*threat*) is inspired by global studies relating land use and threatened species distribution (e.g. Lenzen et al., 2009). This hypothesis proposes that in more heavily used areas, vulnerable species are exposed to more threats than in less modified environments and thus, predicts a positive relationship between agricultural extent, intensity and/or time of human use on the one hand, and the proportion of threatened species on the other. An alternative hypothesis, which we called *shelter*, proposes instead that vulnerable species in heavily used areas are likely to become locally extinct, with remaining populations largely persisting in areas less used by humans, where more quality habitat still persists (Sanderson *et al.*, 2002). Therefore, the *shelter* hypothesis predicts a negative relationship between agricultural extent, intensity and/or time of human use and the proportion of threatened species.

Our main goal is to explore the heterogeneous distribution of threatened species in relation to different levels of agricultural pressure. We focus on areas covered to some extent by croplands to compare gradients of extent and intensity within a single category of land use; and on terrestrial mammals because their conservation status is generally well defined by the IUCN Red List (IUCN, 2014) and because many of them are affected by agriculture (González-Suárez & Revilla, 2014). Namely, we evaluate which of the three types of agricultural metrics: extent, intensity, or history, best predicts threatened mammals' current distributions; and explore the relationship between agricultural indicators and the proportion of threatened mammals to assess the degree of agreement with the two proposed hypotheses – *threat* and *shelter*. We completed analyses at both global and biogeographic-realm scales, given their noticeable differences in terms of land-use history and biodiversity.

Methods

Data sources

We obtained terrestrial mammals distribution maps from the International Union for Conservation of Nature (IUCN, 2014), selecting only native, extant, and probably extant areas. We intersected distribution data with a grid, and species were considered present in a particular grid-cell when any overlap existed. We used a Behrmann cylindrical, equal-area projection, where each grid-cell corresponded to 110 x 110 km (~1º x 1º at the Equator), as finer resolutions are not recommended at the global scale due to the overestimation of species' occurrences (Hurlbert & Jetz, 2007). We calculated the proportion of threatened mammals by grid-cell as the sum of overlapping species classified by the IUCN Red List (IUCN, 2014) as critically endangered, endangered, and vulnerable divided by overlapping total mammal richness. We preferred this measure over the total count of threatened species to account for the expected dependence on total richness and to control for the known environmental gradient in species richness (Torres-Romero & Olalla-Tárraga, 2014). For analyses, we selected cells that contain any level of cropland as defined by Erb et al. (2007) cropland extent map (see below), and that had a land area of at least 10,000 km^2 (to avoid comparing grids with very unequal land areas).

To describe agricultural land use, we considered three groups of metrics: land-use extent, land-use intensity, and land-use history (Table S1.1). We employed the global land-use/cover classification of Erb et al. (2007) to define different proportions of land use within each grid-cell including the categories: cropland, forest, grazing land, urban and infrastructure, and areas without land use (defined as the remaining surface not classified under any of the other categories). We chose this classification for three reasons: all categories sum up to 100% of the grid surface, it is coherent with national census data, and most of the intensity metrics we used are based on this cropland map.

We selected indicators of cropland intensity based on the conceptual framework of Erb et al. (2013) and Kuemmerle et al. (2013), including metrics of inputs (irrigated area and added fertilizers) and outputs (yields of maize, wheat and rice, as well as harvested areas of soy and oil palm; see Table S1.1. for full details on data sources). Input metrics reflect direct potential impacts on the environment, for example on nutrient and water cycles, and are often employed when assessing biodiversity responses to impacts of agriculture (e.g. García de Jalón et al., 2013). Output metrics measure productivity (e.g., yields, as the ratio of land and total production, or energy efficiency) and represent another important facet of the intensity of agriculture that includes indirect threats such as transport and on-site manipulation (Turner & Doolittle, 1978). We selected yields of maize, wheat and rice because these are the globally dominant cereal crops (Hafner, 2003). Representing each crop separately is important to capture regional differences in productivity among areas where one crop may be nearly absent but others are prevalent (Table S1.2). Finally, soy and palm oil crops are increasingly relevant in the tropics, where they are expanding into primary forests where mammal biodiversity is high (Hecht, 2005; Gutiérrez-Vélez *et al.*, 2011). We used available data on harvested area of soybeans and palm oil rather than yields because they have been found to be more consistent across alternative data sources (Fitzherbert *et al.*, 2008; GAEZ, 2010). These are considered an intensity metric because these crops are normally associated to high inputs of fertilizers and overall yields (Fearnside, 2001; Koh & Wilcove, 2008).

To test the importance of agricultural history we included the categorical variable of time of first significant land use (hereafter, time of first use) following the KK10 model (Kaplan *et al.*, 2011), defined as the time at which >20% of a grid-cell is classified as dedicated for any human use (Ellis *et al.*, 2013). Temporal intervals considered in the KK10 model are B.C.6000, B.C.3000, B.C.1000, A.D.0, A.D.1000, A.D.1500, A.D.1750, A.D.1900, A.D.1950 and A.D.2000. The KK10 model includes estimations of area converted for any type of land use (e.g. settlements, grazing lands, etc.) based on population densities and per capita use of land, although it does not explicitly incorporate intensity metrics. This past land-use reconstruction is generally considered more realistic than others available (Ellis *et al.*, 2013; Boivin *et al.*, 2016).

A list of data sources is found in Appendix 1 and further described in Table S1.1. The original resolution of our datasets was varied, thus we recalculated mean values per grid-cell using the Zonal Statistics tool within the Spatial analyst extension in ArcGIS 10.3 (ESRI, 2011).

Statistical analyses

We divided our grid-cells containing any level of cropland (>0) into biogeographic realms (based on a modified classification of Olson et al. (2001) including: Afrotropics (1463 grid-cells), Australasia (300 grid-cells), Indomalay (518 grid-cells), Nearctic (994 grid-cells) and Neotropics (1463 grid-cells). We further subdivided the Palearctic realm into Asia (2078 grid-cells) and Europe (including Morocco and northern Algeria; 926 grid-cells), given their marked differences in terms of human history. All grid-cells that were not fully included in any of the mentioned realms were assigned to the Ecotone category and included in the global model, but not analysed as a separate realm (N=210; grey areas in Fig.2). Madagascar was excluded from the Afrotropics' analysis (but not from the global) given its biogeographic particularities as an island, which situates it as a clear outlier in terms of threatened mammals due to small ranges sizes and high numbers of endemic species (Fig. S1.1A). Using these geographic units enhances our ability to detect patterns without confounding different processes, since the range of variation in land-use extent, intensity and history is specific to each biogeographic realm (e.g., the minimum cover of urban areas in Europe could be the maximum in areas of Australasia). Additionally, they may serve as a space-for-time substitution representing different stages in the agricultural development process.

We performed one global and seven realm-specific models to explore overall and regional relationships. Realm was included as a categorical variable in the global model to account for the expected differences among realms and to avoid pseudoreplication within realms. We used the mean portion of different land-use categories (proved to be equivalent to total proportion per grid-cell; Table S1.3), agricultural intensity metrics and time of first use by grid-cell as predictor variables, and the proportion of threatened mammals as the response, which we arcsine square-root transformed to achieve normality. We included an 'island' dummy explanatory variable for grid-cells included within an island territory ($\geq$10,000 km^2) to account for potential island-specific vulnerability attributes. Australasia is entirely formed by islands, thus we did not include this dummy variable in that realm model. Conservatively, we excluded highly correlated predictors (Spearman's $\rho \geq |0.7|$) to avoid interpretative errors (Olden *et al.*, 2008); we selected only one variable from each correlated pair, omitting the one that correlated with the greatest number of other predictors (Tables S1.5-S1.12).

To analyse data we used a machine-learning approach known as boosted regression trees (BRT). BRT differs from traditional regression methods that produce a single 'best' model by using the technique of boosting to combine large numbers of relatively simple tree models to optimize predictive performance. BRT allow for detecting nonlinear relationships and including variables of very different nature and units (Elith *et al.*, 2008). BRT were fitted using function 'gbm.step' in the *dismo* package (Hijmans *et al.*, 2013) in R version 3.0.3 (R Development Core Team & R Core Team, 2014). This function calculates the optimal number of boosting trees using 10-fold cross validation. We used a Gaussian error structure, a bagging fraction of 0.5, and a tree complexity of 10 (up to 10-way interactions). Learning rate was 0.050 for the global model and 0.001 for the realm-specific models. These parameters were fixed according to the guidelines in Elith et al. (2008) to achieve a minimum of 1,000 trees.

We considered a particular predictor as relevant when its relative importance was greater than expected due to chance (total importance of 100% divided by the number of variables included in each model; Müller et al. 2013). To account for spatial autocorrelation, all models included a residuals-based autocovariate (RAC) that specified the relationship between residual values at each location to those at neighbouring locations (the 8 immediate grid-cells surrounding each cell, approximately within a 165 km distance in our case) from a model excluding spatial autocorrelation. Deriving the autocovariate from the residuals allows for the inclusion of only the unexplained deviance remaining after considering the explanatory variables, thus the actual influence of the predictors is better captured (Crase *et al.*, 2012). The explanatory power of each model was calculated as the percentage of deviance explained respect to a null model, defined as one without any splits – equivalent to an intercept only model in linear regression (Ferrier &

Watson, 1997). The effect of each predictor was described in relation to the fitted model in which all other predictors were set to their average by means of partial dependency plots (PDP).

Finally, in order to improve the interpretability of our results, we tested whether consistency with the two hypotheses could be partially due to the correlation between agriculture and potential confounding factors not included in our analyses. We calculated simple correlations (Spearman's ρ) between our predictors and a pool of environmental and non-land-use anthropogenic indicators typically assessed when exploring species distributions gradients at the global scale (Table S1.4; Torres-Romero & Olalla-Tárraga, 2014).

Results

We completed the analyses on 7,962 grid-cells representing around 61% of the global terrestrial surface excluding Antarctica. A total of 4,780 terrestrial mammals overlapped the selected study area, 18% were classified as threatened, 69% as non-threatened, and 13% as data deficient. Regarding agricultural extent variables, our grid-cells included varying mean proportions of cropland, ranging from <0.01% to 98%, with the Indomalay realm having the highest mean value (40%), and the Neotropics the lowest (7.8%, Table S1.2). Other land-use extent components presented varying proportions: built-up areas represented the lowest extent (global average, 1.2%), and grazing lands the highest (global average, 40.5%). Globally, croplands tended to co-occur with built-up areas and heavily fertilized areas (Spearman's ρ=0.89 and ρ=0.74, respectively) and were moderately disagreeing with non-used portions (ρ=-0.57; Table S1.5), although these correlations varied among realms (Tables S1.6-S1.12). Agricultural intensity metrics also presented quite heterogeneous values among realms, with oil palm and soy presenting very low overall harvested areas (Table S1.2). Indomalay had on average the oldest and Australasia the youngest land-use history.

Model performance was relatively high, with 82.7% deviance explained by the global BRT model, and values ranging from 41.9% (Australasia) to 81.6% (Asia) for the realm-specific BRT models (Table 1). The inclusion of the spatial-autocorrelation term (RAC) improved these values and effectively corrected for spatial autocorrelation effects (as measured by Moran's I in the model residuals) in all models with the exception for Australasia (although even in this case the Moran's I parameter value was improved, Tables 1 vs. S2.1). The RAC was identified as relevant in all models, with an importance ranging from 26.5% (global) to 63.9% (Nearctic, Table 1). No relevant interactions among variables were found (Tables S2.2-S2.9).

Relevance of agricultural indicators

We found differences among models regarding which type of agricultural indicators best predicted threatened mammals' distributions. In the global BRT, the variable contributing most to explain patterns of threatened mammals was realm (35.3% importance, Table 1). The highest proportion of threatened mammals was predicted in the Indomalay realm, followed by the Ecotone (grid-cells belonging to more than one biogeographic realm). The Afrotropics, the Neotropics, and Asia presented similar predicted values, while the Nearctic was predicted to have the lowest portion of threatened mammals (Fig. 1a). Only one land-use extent indicator was identified as relevant globally, forest coverage, with a 7.1% importance (Table 1), with slightly higher proportions of threatened species occurring in less-forested areas (Figs. 1b, S1.1, and S2.1).

In realm-specific BRTs, indicators of land-use extent were important in explaining the share of threatened mammals in Asia, Australasia, Europe, Indomalay, and the Neotropics; cropland intensity was important in the Indomalay and the Neotropics; while agricultural history presented a relevant contribution only in the Indomalay realm (Table 1). No agricultural land-use indicator appeared to explain threatened terrestrial mammals distribution in the Afrotropics and Nearctic realms.

Threat vs. shelter hypotheses

Our results may be interpreted as consistent with both the *shelter* and the *threat* hypotheses varying across scales and realms. In the global model, the *threat* hypothesis seemed endorsed by the negative relationship between forest cover (relevant indicator) and proportion of threatened mammals, although this relationship was not very clear (Fig. 1). Realm-specific results served to disentangle part of this complexity.

Relationships in agreement with those predicted by the *shelter* hypothesis were observed in two realms: Australasia and Indomalay. In these areas higher portions of threatened mammals occurred where the extent and/or intensity of agriculture were relatively low. Namely, in Australasia and the Indomalay realms, areas with higher forest cover were associated with higher proportions of threatened mammals (Fig. 2; variable importance 26.8% and 27.0%, respectively). In the Indomalay realm, wheat yield was also found to be relevant (variable importance 14.4%), with more threatened species in areas of lower intensity (Fig. 2). The relationships predicted by the *threat* hypothesis were observed in Asia and Europe. The single most relevant indicator in both realms was the portion of forest per grid-cell (variable importance 17.0% and 20.2%, respectively), with higher proportions of threatened species found in cells with less forest (Fig. 2).

Finally, results from the Neotropics were consistent with both hypotheses. Relevant variables included maize yield (variable importance 14.5%) and forest area (13.5%), with more threatened mammals occurring in maize-intensive croplands (as expected from the *threat* hypothesis; Fig. 2) and/or in areas with a greater cover of forest (as expected from the *shelter* hypothesis; Fig. 2).

The correlations between our relevant predictors and potential confounding factors (environmental and non-land-use anthropogenic) were high in some cases (Spearman's $\rho \geq |0.7|$; Tables S1.5-1.12). In Australasia, where higher proportions of forest coincided with higher mean annual precipitation and mean annual actual evapotranspiration (AET, Table S1.8); and in the Indomalay realm, where more forested areas received also more mean annual precipitation, were less accessible, and had lower Human Footprint (HF) values; while intensive wheat croplands were associated with lower AET (Table S1.10).

Discussion

Agriculture is a key threat to global biodiversity, but our understanding of which aspects are more closely associated with threatened species distribution and how threat levels vary across the surface of the globe is partial. To our knowledge, our study is the first to systematically investigate the role of different facets of land use within croplands and how they predict the distribution of threatened mammals globally and by biogeographic realm.

Relevance of agricultural indicators

A land-use extent indicator, forest extent, was repeatedly associated with the distribution of threatened mammals. Alongside this, the inclusion of different indicators of agricultural intensity improved our ability to identify which types of croplands were more relevant predictors in each realm and added support to our proposed hypothesis.

Agricultural history was initially considered a promising indicator based on previous findings (Dullinger *et al.*, 2013). However, in our study it was only identified as relevant in the Indomalay realm and the relationship was intricate, with areas first modified in c.A.D. 0, 1900 and 2000 having slightly higher proportions of threatened species (Fig. 2). These patterns are difficult to interpret probably because time since first use may be too simplistic to capture the complexities of land-use legacy at this scale. It would be desirable to know the particular type of land transformation at finer scales to provide a plausible explanation for this pattern. Importantly, in regions like Europe, which have experienced extinction filters (Turvey & Fritz, 2011) and where most sensitive mammals are likely to have already disappeared, the proportion of threatened mammals may be now largely independent from the time since first use and primarily related to relatively recent processes.

Threat vs. shelter hypotheses

Although global patterns were largely in agreement with predictions from the *threat* hypothesis, when disaggregating our analyses by biogeographic realm, we uncovered realm-dependent relationships. Patterns consistent with predictions from the *shelter* hypothesis were found in tropical realms (Indomalay and Australasia, the latter is partially tropical in the current analysis; Fig. 2). In some regions within these realms, like Papua New Guinea in Australasia (Fig. S1.4), or Indonesia and Malaysia in the Indomalay (Fig. S1.6), the relatively large remaining tracts of forest were associated with more threatened terrestrial mammals, as expected if these areas included the remaining population of vulnerable species, as proposed by the *shelter* hypothesis. These forest areas were positively correlated with higher precipitation and higher AET (Australasia, $\rho_{forest\text{-}prec.}$=0.82 and $\rho_{forest\text{-}AET}$=0.86, Table S1.8, Indomalay, $\rho_{forest\text{-}prec.}$=0.74), these environmental factors may influence local species richness and presence of forest, but we do not expect they influence the proportion of threatened mammals. In addition, in the Indomalay realm we found forested areas generally were less accessible and had lower Human Footprint values ($\rho_{forest\text{-}acc.}$=0.74 and $\rho_{forest\text{-}HF.}$=-0.78; Table S1.10), which provides additional hints for the potential *shelter* role of these areas. Nevertheless, forest *shelter* areas are unlikely to be entirely free from threats, and may be affected by wood extraction and other human activities like hunting (Fitzherbert et al., 2008), as well as extinction debts (sensu Kuussaari et al., 2009).

We detected patterns consistent with the predictions from the *threat* hypothesis primarily within temperate realms (Europe and Asia; Fig.2), where agriculture is so widespread that sensitive species are often forced to co-occur within matrices of intensive agricultural land uses. This is the case in Europe, where less forested lands coincided with higher numbers of threatened mammals (Fig. S1.5); these areas are mainly located in southern Europe, where sensitive species remain. In northern Europe, on the contrary, forested areas are mostly secondary species-poor forests, where threatened mammals are absent (Polaina *et al.*, 2015). On the other hand, in Asia, lower forest cover may coincide with a mixture of at least two contrasting types of landscapes: relatively unused lands with a high level of endemism and threatened species, like the Tibetan Plateau (Fig. S1.3; Tang *et al.*, 2006); and intensive croplands where species are more exposed to agricultural human pressures (like wheat crops; Fig. S2.3). However, there was not a clear preponderance of any type of land use and that may be why no additional indicator appeared as relevant in our models, leading to a weaker overall agreement with the *threat* pattern.

Finally, a peculiar case in our results was the Neotropics, where higher proportions of threatened terrestrial mammals tended to coincide with the large forested area of the Amazon, but also with the Andean maize belt (Figs. S1.8 and S2.8), a region containing recognized hotspots of endemism but also extensive agricultural lands (Leff *et al.*, 2004); thus showing patterns consistent with predictions from both *shelter* and *threat* hypotheses. This may be a consequence of the size and heterogeneity of this realm. In the Nearctic and the Afrotropics, agricultural land-use indicators were not associated with threatened species richness distribution and the spatial autocovariate showed high values, which suggests other factors not considered in the present study are associated with threatened mammals' distribution within croplands on this realm.

A unifying hypothesis?

It is often assumed that threat levels, pressure from agriculture in our case, correspond to higher shares of threatened species. Our analyses show that this relationship might not be so straightforward and varies in important ways with the history of anthropogenic pressure in a territory. Even if agricultural land-use history by itself was not hugely relevant in our study, separating analyses by realm indirectly differentiates territories at different agricultural development stages and, accordingly, geographical differences consistent with predictions from both *threat* and *shelter* hypotheses were found. In light of these results, we propose a complex non-linear relationship between agricultural land use on the proportion of threatened species, described by dampening cycles, involving three broad stages (Fig. 3).

Under this hypothesis, expanding agricultural systems would initially generate patterns in line with the *threat* hypothesis; the proportion of threatened species would increase due to the rise in threatening activities. In this initial stage, extinction would be very limited, so total species richness would remain nearly constant, while the number of threatened species increases (Fig. 3a). Next, with further development, extinctions would occur, and threatened mammal richness will decrease more rapidly than the total species richness, resulting in an overall decrease in the proportion of threatened mammals. Only areas with at least partly suitable land use conditions would retain sensitive (threatened) species, thus showing patterns consistent with the *shelter* hypothesis (Fig. 3b). Finally, as development continues, the remaining sensitive species may be lost, causing a second wave of defaunation, while other species still present in the area may become threatened (due to persistent or new threats) leading to a rise in the proportion of threatened species and a new positive relationship consistent with the *threat* hypothesis. At this stage, differences in the proportion of threatened species would be less pronounced as overall richness would be reduced (sensitive species have already been lost) and persisting species would be expected to be more resistant/adapted to cohabit with humans (Fig. 3c).

Caveats and challenges

The results and inferences presented here have some limitations. First, our study was too broad scale to assess the causal relationship between land use and biodiversity. Rather, we show what predictors are most strongly related to threatened species distributions. Finer scale work could delve into our proposed hypotheses and better test their validity. For example, intra-realm variability could be explored at finer scales, particularly in large and heterogeneous realms. Second, the proposed continuous global hypothesis is based on assuming a valid space-for-time substitution in how land use influences biodiversity, since global time-series for the indicators presented here are not currently available and experimental manipulations are not possible. Finally, our study cannot account for lagged time effects or extinction debts or data quality limitations, but still can served to highlight areas where high concentrations of threatened species in apparent *shelter* regions exist. Global data describing distribution ranges and land use are likely to include heterogeneity in quality and precision (when data were captured and to what level of detail). Some areas in which we reported high proportions of threatened species may already have lost some species, but that information is not yet available. On the other hand, additional factors –likely environmental– may play a role in explaining distribution of threatened mammals worldwide (included in the RAC), however, the mechanism to influence threatened species is not expected to be straightforward and would require different analytical approaches. Together, these issues underline the challenges inherent in implying any form of causality between our predictor variables and our biodiversity distributions.

From a practical conservation perspective, our results present a challenge in that low proportions of threatened species may represent at least two distinct processes: few ongoing threats or past extinction of sensitive species, each leading to different conservation values and management implications (Polaina *et al.*, 2015). Our study aims to highlight the land-use attributes of areas where high proportions of threatened species still exist, and we considered the context of the different regions to interpret our results. However, more detailed studies that include data on local extinctions and that incorporate long-term time-series data would be necessary to disentangle these two processes. For example, multispecies long-term monitoring data or information on historical distributions within a particular site might offer the opportunity to evaluate the mechanisms behind our proposed continuous hypothesis, however these data are rarely available and may present quality issues (but see Boakes *et al.*, 2017).

Conclusions

This study provides a first global perspective of the complex relationships between agricultural land use, namely croplands, and threats to mammal biodiversity, in terms of agricultural extent, intensity and history. Arguably, the proposed unifying hypothesis could also be useful to contextualize the distribution of other important global threats for mammals, such as overexploitation or invasive species, in which non-linear relationships may also occur. In addition, our results open a way towards a better understanding of the potential consequences of future agricultural land-use changes and the design of more context-specific conservation strategies. For example, areas where future cropland expansion is expected to occur, currently show vulnerable species remaining in potential *shelter* areas that may be further transformed, suggesting a high risk of biodiversity loss (Laurance *et al.*, 2014; Kehoe *et al.*, 2017a). Conservation actions to protect mammalian fauna in *shelter* areas would require to jointly considering croplands and forest patches, questioning traditional models of cropland expansion and intensification which could condemn numerous terrestrial mammal species. On the other hand, within the *threat* areas, remaining threatened species may require active conservation strategies to persist in highly modified environments. On the plus side, socioeconomic changes such as farmland abandonment due to emigration from rural areas, could bring region-specific opportunities for regeneration (Navarro & Pereira, 2012; Beilin *et al.*, 2014).

Our results suggest that understanding the stage of agricultural transition is key to correctly interpret biodiversity loss patterns. While useful in our study, the employed biogeographic realms may not the most suitable assemble to understand different land-use transitions. Specific metrics that better characterize the transition stage of each region of the world are urgently needed in order to propose conservation actions adapted to the particularities of each region and to maximize biodiversity protection. Additionally, closer monitoring of long-term temporal trends within specific areas will improve the understanding of the fate of regional biodiversity.

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Data accessibility

All data employed on the present work are public and can be downloaded from the original sources (Appendix 1).

Biosketch

Ester Polaina works to understand current distribution of biodiversity and how human activities influence that spatial configuration. She is interested in finding a balance between socioeconomic development and natural systems' conservation at different scales and using different approaches.

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Appendix 1 – Data sources

Land-use extent

Erb, K., Gaube, V. & Krausmann, F. (2007) Research Article A comprehensive global 5 min resolution land-use data set for the year 2000 consistent with national census data. **2**, 191–224.

Land-use intensity

Monfreda, C., Ramankutty, N. & Foley, J. a. (2008) Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles*, **22**, 1–19.

Potter, P., Ramankutty, N., Bennett, E.M. & Donner, S.D. (2010) Characterizing the spatial patterns of global fertilizer application and manure production. *Earth Interactions*, **14**, 1–22.

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Land-use history

Ellis, E.C., Kaplan, J.O., Fuller, D.Q., Vavrus, S., Klein Goldewijk, K. & Verburg, P.H. (2013) Used planet: A global history. *Proceedings of the National Academy of Science*, **110**, 1–8.

Environmental indicators

Fick, S. & Hijmans, R.J. (2017) WorldClim2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, **37**, 4302–4315.

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Non-land-use anthropogenic indicators

Nelson, A. (2008) Estimated travel time to the nearest city of 50,000 or more people in year 2000. *Global Environment Monitoring Unit-Joint Research Centre of the European Comission*.

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Tables

Table 1. Results of the BRT models, global and by realm. *Afro.* = Afrotropics; *Austr.* = Australasia; *Indo.* = Indomalay; *Neotrop.* = Neotropics. *Moran's I* was calculated for the residuals of each cell and the grid-cells surrounding it (all adjacent neighbours; max=8). *RAC,* residuals spatial autocovariate. Bold numbers indicate variables considered as relevant (i.e. their importance is greater than the expected under uniformity; thresholds are indicated in the last row).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
No. trees	1400	8000	6300	3300	6350	4850	4300	4650
Residuals Moran's I	-0.04	-0.05	-0.04	0.12***	-0.05	-0.01	-0.03	-0.05
% Deviance explained	82.68	61.95	81.62	41.86	79.76	76.37	65.25	63.15
Variables (importance, %)								
Land-use extent								
Built-up	~	~	~	3.86	~	~	~	~
Cropland	3.12	5.69	4.55	~	1.79	~	6.13	6.93
Forest	**7.14**	4.58	**17.06**	**26.82**	**20.25**	**27.05**	3.33	**13.50**
Grazing land	2.77	~	2.85	5.65	2.53	2.55	2.81	7.50
Not used	2.15	6.32	2.16	3.79	3.14	~	2.76	2.40
Land-use intensity								
Fertilizer	~	4.67	~	4.39	6.09	5.22	~	~
Irrigated area	2.32	2.75	~	4.04	8.93	~	2.57	2.44
Maize	2.52	5	~	4.19	~	2.62	2.54	**14.53**
Rice	5.99	8.15	~	0.97	5.50	4.34	0	1.52
Wheat	2.94	5.94	8.08	~	~	**14.39**	7.25	3.25
Oil palm	0.48	4.91	-	0.72	-	2.33	-	0.08
Soy	1.21	1.83	1.96	0.19	6.42	6.98	2.92	6.78
Land-use history								
Time of first use	4.7	6.22	8.9	5.62	9.02	**12.76**	5.71	2.23
Island	2.77	-	0.01	-	0.14	0.58	-	0
Realm	**35.33**	**-**	-	-	-	-	-	-
RAC	**26.55**	**43.95**	**54.44**	**39.76**	**36.19**	**21.18**	**63.98**	**38.84**
Relevance threshold	*7.14*	*8.33*	*11.11*	*8.33*	*9.09*	*9.09*	*9.09*	*7.69*

*** p<0.001, spatial autocorrelation exists; -, not existent/applicable; ~, variable excluded because its correlation with other/s was ≥|0.7| (Spearman's ρ).

Figures

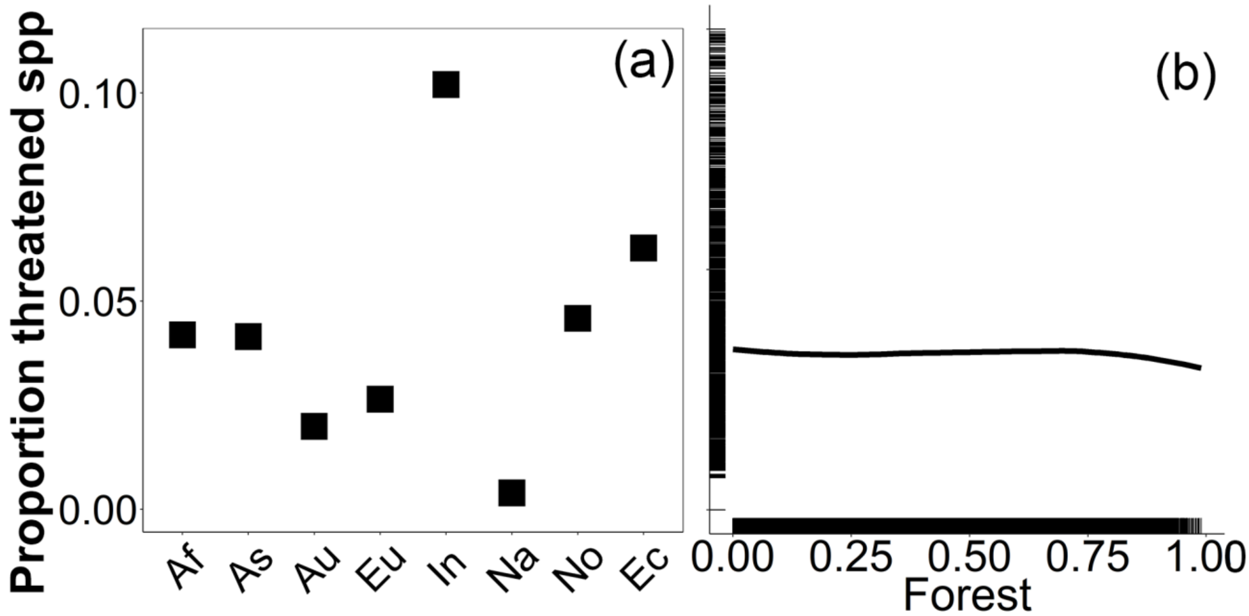
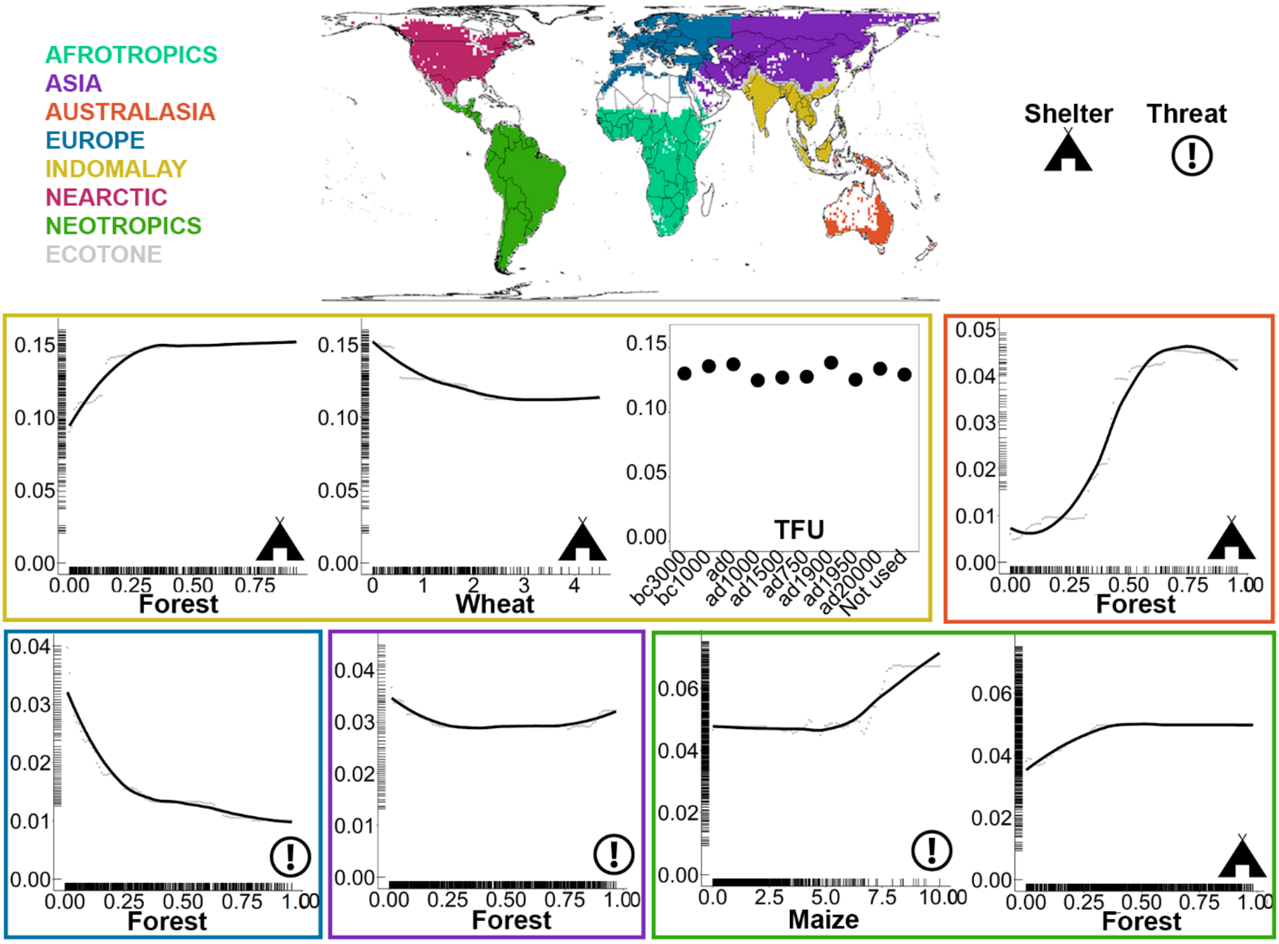


Figure 1. Partial dependency plots of relevant predictors in the global BRT model; (a) biogeographic realm (35.33% importance) and (b) forest extent (7.14% importance). *Af* = Afrotropics; *As* = Asia; *Au* = Australasia; *Eu* = Europe; *In* = Indomalay; *Na* = Nearctic; *No* = Neotropics; *Ec* = Ecotone.



724

725 **Figure 2.** Partial dependency plots (PDP) of relevant predictors of the realms BRT models. Colour
726 legend matches realms' names, map and PDPs' borders. Y-axis in all plots represents predicted
727 proportion of threatened mammals. Symbols illustrate the matching hypothesis for each predictor
728 (*threat* or *shelter). TFU* refers to the time period of first significant land use.

729

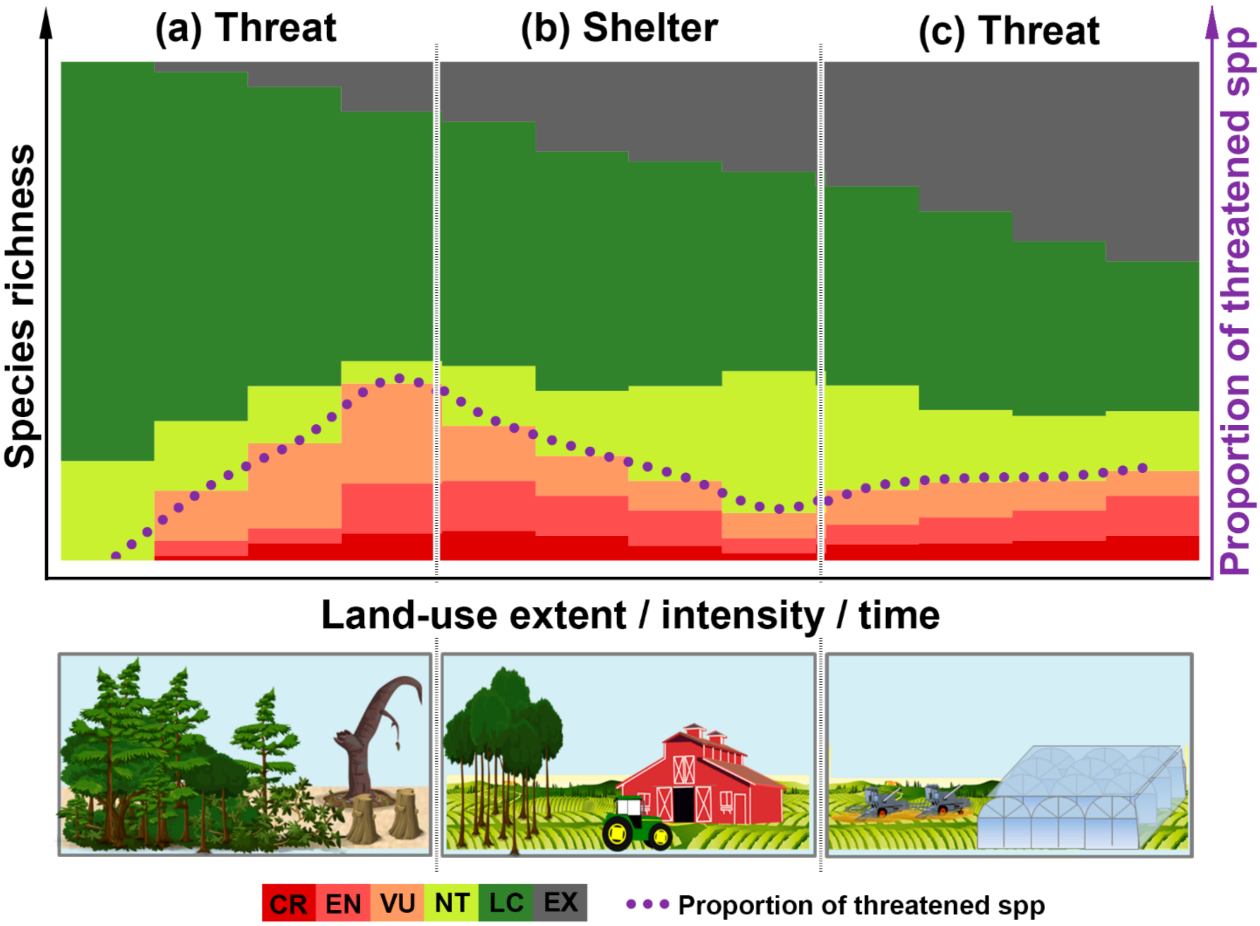


Figure 3. Schematic representation of the continuous hypothesis proposed. The X-axis represents land-use extent, intensity or time since first use within a certain area. The Y-axis (left) represents species richness where each colour indicates the number of species in each category; greenish colours represent non-threat categories, reddish colours mark threat categories. Legend: *CR*, critically endangered; *EN*, endangered; *VU*, vulnerable; *NT*, near threatened; *LC*, least concern; *EX*, extinct. The Y-axis (right) represents the proportion of threatened species, marked by the purple dotted line.

Supporting Information

Appendix S1. SUPPLEMENTARY DATA DESCRIPTION

Table S1.1. Description and sources of indicators of land use extent, intensity and history. Short name is used in the main manuscript.

Indicators *Long name*	*Short name*	Units, description	Year	Original resolution	Data sources	Reference
Land-use extent						
Urban and infrastructure	Built-up	% grid-cell	2000	5 min	Eurostat, national inventories, GLC2000	Erb *et al.* (2007)
Cropland	Cropland	% grid-cell	2000	5 min	Ramankutty & Foley (1999), FAO	Erb *et al.* (2007)
Forest	Forest	% grid-cell	2000	5 min	FRA2000, GLC2000	Erb *et al.* (2007)
Grazing land	Grazing land	% grid-cell	2000	5 min	GLC2000	Erb *et al.* (2007)
Areas without land use	Not used	% grid-cell	2000	5 min	Human footprint (Sanderson et al. 2002), GLC 2000	Erb *et al.* (2007)
Land-use intensity						
Inputs						
Industrial and manure fertilizer application rates (N, P)	Fertilizer	kg/ha	1994 - 2001	10 km	FAO “Fertilizer Use by Crop 2002” combined with harvested area for 175 crops (Monfreda et al. 2008).	Potter *et al.* (2010)
Land equipped for irrigation	Irrigated area	% grid-cell	2000	5 min	FAO, World Bank and other international organizations, USGC-GLCC-2.0 and JRC-GLC2000	Siebert *et al.*, (2015)
Outputs						
Yields for rice, wheat and maize	Maize, rice and wheat	tons/ha	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda *et al.* (2008)
Harvested area for soy and oil palm	Soy and oil palm	% grid-cell	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda *et al.* (2008)
Land-use history						
Time period of first significant land use[1]	Time of first use	year (categorical)	-	5 min	KK10 model (Kaplan et al. 2011)	Ellis *et al.* (2013)

[1] Categories: BC6000, BC3000, BC1000, AD0, AD1000, AD1500, AD1750, AD1900, AD1950, AD2000, Not used.

Table S1.2. Global and realm-specific summary of indicators of land-use extent, intensity and history, and mammal diversity. All values represent the mean proportion value within each grid-cell of ~110x110 km. Time of first use was converted to continuous for this purpose.

Indicators	Mean values per grid-cell							
	Global	Afrotropics	Asia	Australasia	Europe	Indomalay	Nearctic	Neotropics
Land-use extent (portion of grid-cell)								
Built-up[1]	0.012	0.005	0.008	0.004	0.032	0.018	0.025	0.003
Cropland[1]	0.141	0.095	0.088	0.126	0.255	0.400	0.178	0.078
Forest[1]	0.319	0.300	0.254	0.239	0.319	0.326	0.325	0.447
Grazing land[1]	0.405	0.558	0.432	0.460	0.304	0.245	0.328	0.375
Not used[1]	0.123	0.042	0.218	0.171	0.091	0.011	0.145	0.096
Land-use intensity								
Inputs								
Fertilizer[2] (kg/ha)	6.167	0.552	6.351	2.452	10.915	18.622	8.767	1.927
Irrigated area[3] (portion of grid-cell)	2.470	0.312	2.628	0.496	2.810	12.516	2.326	0.624
Outputs								
Maize[4] (tons/ha)	1.703	0.820	1.226	1.568	2.445	1.831	3.419	1.663
Rice[4] (tons/ha)	1.103	1.002	1.129	0.801	0.678	2.712	0.130	1.411
Wheat[4] (tons/ha)	1.052	0.965	0.884	0.514	1.732	1.045	1.709	0.521
Oil palm[4] (portion of grid-cell)	0.001	0.002	-	<0.001	-	0.005	-	<0.001
Soy[4] (portion of grid-cell)	0.007	0.000	0.003	0.000	0.001	0.011	0.024	0.014
Land-use history								
Time of first use[5] (years)	626	1185	329	1374	120	-315[6]	1127	651
Mammal diversity								
Total richness	78.1	106.4	45.5	42.5	49.0	95.0	58.3	130.8
Threatened spp.	4.1	4.4	2.4	1.5	1.5	14.3	0.4	6.8
(%)	5%	4%	5%	3%	3%	15%	1%	5%

[1]Erb et al. (2007); [2]Potter et al. (2010); [3]Siebert et al. (2015); [4]Monfreda et al. (2008); [5]Ellis et al. (2013); [6]B.C.315

Table S1.3. Correlations (Spearman's rank coefficient, ρ) between mean portion and total portion per grid of the land-use categories included in the analyses.

	Spearman's ρ
Built-up	0.99
Cropland	0.99
Forest	0.97
Grazing land	0.96
Not used	0.99

Table S1.4. Description and sources of environmental and non-land-use anthropogenic indicators tested for correlation with our land-use predictors.

Indicators		Units, description	Year	Original resolution		References
Long name	*Short name*			*Spatial*	*Temporal*	
Environmental						
Mean annual actual evapotranspiration	AET	mm, accumulated	2000	1 degree	month	Zhang *et al.* (2010, 2015)
Mean annual temperature	Temperature	ºC, average	1970-2000	10 arc minutes	month	Fick & Hijmans (2017)
Mean annual precipitation	Precipitation	mm, average	1970-2000	10 arc minutes	month	Fick & Hijmans (2017)
Global digital elevation model	Elevation	m	1996	30 arc seconds	-	LP DAAC (2004)
Crop suitability index for high input level rain-fed cereals	Crop suitability	index [0-10,000]	1961-1990	5 arc minutes	-	Fischer *et al.* *(*2012)
Non-land-use anthropogenic						
Travel time to major cities (≥50,000 people)	Accessibility	minutes	2000	30 arc seconds	-	Nelson (2008)
Global Human Footprint	Human footprint	index [0-10]	1995-2004	1 km	-	Sanderson *et al.*, (2002)

Table S1.5. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the global BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.89																	
Forest	0.07	-0.01																
Grazing land	-0.01	0.03	-0.55															
Not used	-0.55	-0.57	-0.22	-0.10														
Irrigated area	0.61	0.62	-0.21	0.19	-0.39													
Fertilizer*	0.69	0.74	-0.09	0.09	-0.49	0.76												
Wheat yield	0.51	0.49	-0.18	0.21	-0.37	0.57	0.63											
Maize yield	0.57	0.60	-0.02	0.14	-0.45	0.61	0.74	0.63										
Rice yield	0.23	0.34	0.06	0.12	-0.29	0.37	0.42	0.22	0.45									
Oil palm	-0.03	0.01	0.22	-0.01	-0.17	-0.10	0.00	-0.14	0.03	0.27								
Soy	0.48	0.52	0.07	-0.03	-0.40	0.45	0.58	0.43	0.59	0.34	-0.02							
AET	0.13	0.22	0.47	-0.19	-0.26	0.00	0.18	0.02	0.29	0.41	0.38	0.22						
Temperature	-0.07	0.14	0.03	0.11	-0.22	0.06	0.14	-0.10	0.12	0.44	0.31	0.01	0.50					
Precipitation	0.17	0.23	0.63	-0.32	-0.30	-0.02	0.17	-0.05	0.22	0.41	0.40	0.24	0.82	0.47				
Elevation	-0.15	-0.19	-0.18	0.26	0.13	0.06	-0.07	0.18	0.04	0.02	-0.01	-0.12	-0.17	-0.22	-0.23			
Human Footprint	0.72	0.76	-0.06	0.19	-0.62	0.71	0.77	0.57	0.65	0.43	0.09	0.51	0.21	0.19	0.21	-0.07		
Accessibility	-0.68	-0.69	0.11	-0.19	0.56	-0.68	-0.70	-0.52	-0.58	-0.20	0.07	-0.46	-0.07	-0.13	-0.06	0.16	-0.84	
Crop suitability	0.37	0.46	0.27	-0.06	-0.46	0.10	0.31	0.23	0.36	0.22	0.15	0.33	0.54	0.39	0.52	-0.39	0.43	-0.42

*excluded predictors in the BRT model.

Table S1.6. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Afrotropics BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.84																	
Forest	-0.01	-0.09																
Grazing land	-0.09	-0.08	-0.75															

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
No used	-0.15	-0.10	-0.42	0.29														
Irrigated area	0.46	0.46	-0.28	0.16														
Fertilizer	0.53	0.62	-0.34	0.23	-0.01	0.58												
Wheat yield	0.15	0.13	-0.12	0.16	-0.03	0.16	0.21											
Maize yield	0.53	0.55	-0.14	0.12	-0.06	0.45	0.63	0.31										
Rice yield	0.41	0.45	-0.01	0.07	-0.09	0.30	0.52	0.11	0.61									
Oil palm	0.05	0.02	0.49	-0.45	-0.31	-0.15	-0.20	-0.20	-0.07	0.05								
Soy	0.32	0.36	0.03	-0.13	-0.14	0.29	0.41	0.28	0.32	0.20	0.11							
AET	0.03	-0.10	0.76	-0.59	-0.25	-0.28	-0.40	-0.08	-0.14	-0.10	0.43	0.08						
Temperature	-0.18	0.02	-0.16	0.13	-0.06	-0.07	-0.01	-0.44	-0.23	0.01	0.00	-0.23	-0.37					
Precipitation	0.04	0.04	0.77	-0.64	-0.32	-0.25	-0.28	-0.26	-0.07	0.02	0.60	0.11	0.83	-0.12				
Elevation	0.12	-0.02	-0.05	0.06	0.14	-0.01	-0.01	0.44	0.16	-0.07	-0.14	0.08	0.17	-0.84	-0.04			
Human Footprint	0.59	0.64	0.04	-0.06	-0.28	0.45	0.50	0.03	0.37	0.39	0.13	0.29	-0.03	0.10	0.15	-0.09		
Accessibility	-0.50	-0.50	0.10	-0.08	0.23	-0.50	-0.50	-0.04	-0.37	-0.32	-0.06	-0.35	0.16	-0.09	0.06	0.13	-0.70	
Crop suitability	0.15	0.25	0.44	-0.29	-0.13	-0.08	0.03	0.01	0.14	0.23	0.09	0.05	0.39	0.05	0.42	-0.11	0.23	-0.10

*excluded predictors in the BRT model.

Table S1.7. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Asia BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area*	Fertilizer*	Wheat yield	Maize yield*	Rice yield*	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.95																
Forest	0.37	0.28															
Grazing land	0.11	0.16	-0.50														
Not used	-0.65	-0.66	-0.20	-0.46													
Irrigated area*	0.54	0.61	-0.18	0.32	-0.47												
Fertilizer*	0.59	0.65	-0.09	0.27	-0.56	0.82											
Wheat yield	0.45	0.51	-0.18	0.33	-0.46	0.73	0.86										

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area*	Fertilizer*	Wheat yield	Maize yield*	Rice yield*	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Maize yield*	0.52	0.57	-0.05	0.17	-0.46	0.74	0.87	0.83									
Rice yield*	0.39	0.44	-0.13	0.20	-0.39	0.69	0.73	0.73	0.82								
Soy	0.54	0.59	0.14	0.10	-0.54	0.63	0.78	0.69	0.75	0.59							
AET	0.40	0.37	0.35	-0.16	-0.23	0.22	0.35	0.38	0.36	0.26	0.43						
Temperature	0.32	0.43	-0.47	0.37	-0.39	0.67	0.67	0.51	0.54	0.53	0.41	-0.06					
Precipitation	0.51	0.47	0.69	-0.27	-0.31	0.10	0.22	0.18	0.24	0.18	0.39	0.59	-0.17				
Elevation	-0.24	-0.20	-0.30	0.15	0.16	0.11	0.09	0.28	0.15	0.17	0.01	0.00	0.00	-0.20			
Human Footprint	0.62	0.68	-0.10	0.40	-0.67	0.83	0.86	0.75	0.74	0.64	0.69	0.31	0.68	0.17	0.03		
Accessibility	-0.62	-0.66	0.08	-0.34	0.65	-0.70	-0.72	-0.51	-0.58	-0.47	-0.57	-0.16	-0.72	-0.11	0.21	-0.84	
Crop suitability	0.62	0.60	0.25	0.14	-0.60	0.38	0.53	0.37	0.46	0.27	0.47	0.39	0.34	0.39	-0.35	0.53	-0.61

*excluded predictors in the BRT model.

Table S1.8. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Australasia BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up	Cropland*	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland*	0.90																	
Forest	0.26	0.12																
Grazing land	-0.11	0.02	-0.45															
No used	-0.67	-0.53	-0.58	0.19														
Irrigated area	0.61	0.62	0.17	0.08	-0.47													
Fertilizer	0.65	0.71	0.17	0.10	-0.46	0.58												
Wheat yield*	0.68	0.77	0.08	0.10	-0.36	0.70	0.76											
Maize yield	0.57	0.51	0.55	-0.30	-0.61	0.53	0.48	0.51										
Rice yield	0.34	0.19	0.42	-0.42	-0.54	0.13	0.13	-0.04	0.54									
Oil palm	0.04	-0.17	0.60	-0.48	-0.40	-0.30	-0.17	-0.46	0.32	0.66								
Soy	0.34	0.38	0.19	0.03	-0.31	0.57	0.49	0.40	0.46	0.22	-0.12							
AET	0.38	0.22	0.86	-0.45	-0.60	0.28	0.28	0.12	0.70	0.53	0.62	0.25						
Temperature	-0.56	-0.62	0.11	-0.24	0.36	-0.45	-0.47	-0.64	-0.21	0.00	0.36	-0.23	0.14					

	Built-up	Cropland*	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Precipitation	0.31	0.16	0.82	-0.52	-0.54	0.24	0.20	0.06	0.65	0.49	0.63	0.19	0.95	0.26				
Elevation	0.02	0.00	0.36	-0.22	-0.15	-0.10	-0.06	-0.05	0.21	0.03	0.23	-0.03	0.34	0.00	0.34			
Human Footprint	0.78	0.66	0.30	0.06	-0.78	0.61	0.55	0.56	0.57	0.39	0.13	0.32	0.40	-0.57	0.31	0.00		
Accessibility	-0.58	-0.65	0.08	-0.31	0.29	-0.74	-0.65	-0.81	-0.29	0.20	0.58	-0.40	0.00	0.58	0.06	0.14	-0.57	
Crop suitability	0.40	0.33	0.49	-0.16	-0.45	0.46	0.50	0.48	0.50	0.16	0.10	0.27	0.63	0.02	0.62	-0.05	0.42	-0.42

*excluded predictors in the BRT model.

Table S1.9. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Europe BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield*	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.77																
Forest	0.07	-0.12															
Grazing land	0.02	0.05	-0.50														
Not used	-0.43	-0.49	-0.43	0.27													
Irrigated area	0.48	0.63	-0.33	0.35	-0.15												
Fertilizer	0.73	0.70	-0.05	0.13	-0.31	0.63											
Wheat yield*	0.83	0.74	0.01	0.09	-0.38	0.55	0.87										
Maize yield*	0.73	0.71	-0.01	0.09	-0.36	0.60	0.78	0.82									
Rice yield	0.23	0.45	-0.25	0.19	-0.05	0.55	0.30	0.27	0.38								
Soy	0.41	0.43	0.08	-0.01	-0.30	0.31	0.23	0.39	0.45	0.21							
AET	0.68	0.64	0.04	0.07	-0.30	0.52	0.63	0.71	0.71	0.40	0.46						
Temperature	0.09	0.27	-0.68	0.27	0.14	0.54	0.35	0.24	0.27	0.39	-0.07	0.21					
Precipitation	0.40	0.17	0.63	-0.22	-0.35	-0.02	0.39	0.45	0.32	-0.09	0.10	0.35	-0.33				
Elevation	-0.18	-0.06	-0.07	0.17	0.09	0.17	0.10	-0.01	0.14	0.17	-0.15	-0.05	0.28	0.10			
Human Footprint	0.85	0.81	-0.07	0.18	-0.38	0.62	0.82	0.86	0.76	0.31	0.37	0.71	0.27	0.34	-0.03		
Accessibility	-0.78	-0.74	0.04	-0.09	0.44	-0.53	-0.75	-0.79	-0.64	-0.18	-0.28	-0.58	-0.27	-0.31	0.15	-0.86	
Crop suitability	0.61	0.64	0.22	-0.13	-0.58	0.18	0.37	0.53	0.47	0.03	0.54	0.42	-0.19	0.25	-0.39	0.55	-0.59

*excluded predictors in the BRT model.

Table S1.10. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Indomalay BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland*	Forest	Grazing land	Not used*	Irrigated area*	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland*	0.91																	
Forest	-0.65	-0.72																
Grazing land	-0.42	-0.49	-0.04															
Not used*	-0.38	-0.43	0.04	0.73														
Irrigated area*	0.77	0.79	-0.73	-0.25	-0.25													
Fertilizer	0.71	0.66	-0.56	-0.20	-0.15	0.72												
Wheat yield	0.46	0.46	-0.48	-0.27	-0.29	0.61	0.47											
Maize yield	-0.09	-0.10	0.12	0.25	0.24	-0.10	0.03	-0.37										
Rice yield	0.13	0.01	0.08	0.06	0.08	0.10	0.25	-0.13	0.50									
Oil palm	-0.42	-0.31	0.34	0.14	0.19	-0.51	-0.26	-0.59	0.31	0.01								
Soy	0.18	0.13	0.00	0.01	-0.08	0.17	0.21	0.18	0.17	0.06	-0.16							
AET	-0.48	-0.50	0.62	0.13	0.21	-0.60	-0.37	-0.72	0.33	0.29	0.65	-0.18						
Temperature	0.09	0.24	-0.37	0.06	0.04	0.10	-0.06	-0.15	-0.11	-0.34	0.22	-0.24	-0.13					
Precipitation	-0.41	-0.52	0.74	0.02	0.12	-0.64	-0.30	-0.58	0.15	0.19	0.51	-0.06	0.78	-0.27				
Elevation	-0.27	-0.30	0.40	0.03	-0.03	-0.25	-0.33	-0.11	0.13	0.07	-0.12	0.18	0.05	-0.63	0.08			
Human Footprint	0.81	0.82	-0.78	-0.18	-0.21	0.85	0.71	0.50	-0.08	0.00	-0.44	0.13	-0.57	0.22	-0.59	-0.31		
Accessibility	-0.79	-0.78	0.74	0.21	0.26	-0.82	-0.63	-0.56	0.08	-0.04	0.58	-0.15	0.62	-0.13	0.63	0.21	-0.89	
Crop suitability	0.58	0.69	-0.51	-0.25	-0.31	0.51	0.32	0.16	-0.10	-0.19	-0.15	0.05	-0.30	0.52	-0.36	-0.37	0.65	-0.62

*excluded predictors in the BRT model.

Table S1.11. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Nearctic BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.96																
Forest	-0.21	-0.25															

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Grazing land	0.16	0.15	-0.49														
Not used	-0.72	-0.69	0.01	-0.25													
Irrigated area	0.49	0.48	-0.29	0.61	-0.51												
Fertilizer*	0.86	0.88	-0.34	0.29	-0.62	0.57											
Wheat yield	0.62	0.61	-0.24	0.45	-0.53	0.65	0.71										
Maize yield	0.66	0.64	-0.36	0.42	-0.61	0.60	0.69	0.68									
Rice yield	0.15	0.14	0.10	-0.02	-0.19	0.22	0.15	0.09	0.14								
Soy	0.71	0.68	-0.13	-0.02	-0.60	0.27	0.63	0.48	0.62	0.18							
AET	0.72	0.70	0.13	-0.16	-0.60	0.20	0.58	0.40	0.44	0.26	0.73						
Temperature	0.44	0.43	-0.18	0.57	-0.58	0.66	0.43	0.56	0.54	0.26	0.39	0.33					
Precipitation	0.31	0.27	0.45	-0.52	-0.26	-0.17	0.12	0.02	0.06	0.23	0.55	0.62	0.08				
Elevation	-0.35	-0.32	-0.09	0.42	0.17	0.23	-0.21	-0.07	-0.12	-0.23	-0.53	-0.62	-0.05	-0.61			
Human Footprint	0.84	0.79	-0.04	0.22	-0.80	0.55	0.75	0.67	0.69	0.21	0.74	0.72	0.65	0.42	-0.34		
Accessibility	-0.78	-0.73	0.14	-0.35	0.73	-0.59	-0.71	-0.65	-0.66	-0.21	-0.63	-0.62	-0.72	-0.28	0.29	-0.90	
Crop suitability	0.74	0.73	-0.05	-0.14	-0.52	0.12	0.66	0.41	0.47	0.15	0.74	0.76	0.22	0.46	-0.60	0.64	-0.58

*excluded predictors in the BRT model.

Table S1.12. Spearman's rank coefficient of correlation (ρ) for all pairs of variables included in the Neotropics BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.85																	
Forest	-0.18	-0.23																
Grazing land	0.35	0.38	-0.77															
Not used	-0.56	-0.59	-0.06	-0.31														
Irrigated area	0.59	0.54	-0.40	0.59	-0.49													
Fertilizer*	0.61	0.53	-0.19	0.37	-0.51	0.71												
Wheat yield	0.27	0.30	-0.37	0.45	-0.20	0.45	0.45											

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Maize yield	0.46	0.46	-0.35	0.50	-0.35	0.53	0.64	0.61										
Rice yield	0.48	0.35	-0.05	0.24	-0.34	0.45	0.62	0.37	0.53									
Oil palm	0.30	0.06	-0.07	0.14	-0.15	0.21	0.37	0.13	0.08	0.34								
Soy	0.35	0.49	-0.12	0.21	-0.34	0.31	0.48	0.40	0.59	0.42	-0.04							
AET	-0.37	-0.40	0.64	-0.78	0.29	-0.55	-0.39	-0.42	-0.61	-0.23	-0.04	-0.30						
Temperature	-0.36	-0.44	0.57	-0.57	0.21	-0.57	-0.43	-0.59	-0.57	-0.21	-0.01	-0.31	0.63					
Precipitation	-0.28	-0.42	0.54	-0.66	0.28	-0.52	-0.33	-0.38	-0.55	-0.17	0.14	-0.25	0.71	0.64	1.00	-0.41		
Elevation	0.31	0.20	-0.35	0.34	-0.09	0.43	0.29	0.31	0.37	0.16	0.13	0.06	-0.50	-0.65	-0.41	1.00		
Human Footprint	0.66	0.62	-0.38	0.62	-0.61	0.80	0.84	0.45	0.64	0.54	0.30	0.42	-0.51	-0.51	-0.49	0.33		
Accessibility	-0.59	-0.63	0.44	-0.65	0.57	-0.74	-0.74	-0.36	-0.67	-0.43	-0.07	-0.50	0.59	0.49	0.61	-0.27	-0.89	
Crop suitability	-0.08	0.07	0.01	0.03	-0.07	-0.13	0.06	0.09	0.17	0.15	-0.12	0.42	0.04	0.25	-0.01	-0.50	0.06	-0.16

*excluded predictors in the BRT model.

Maps of proportion of threatened mammals and relevant indicators globally, and by biogeographic realm

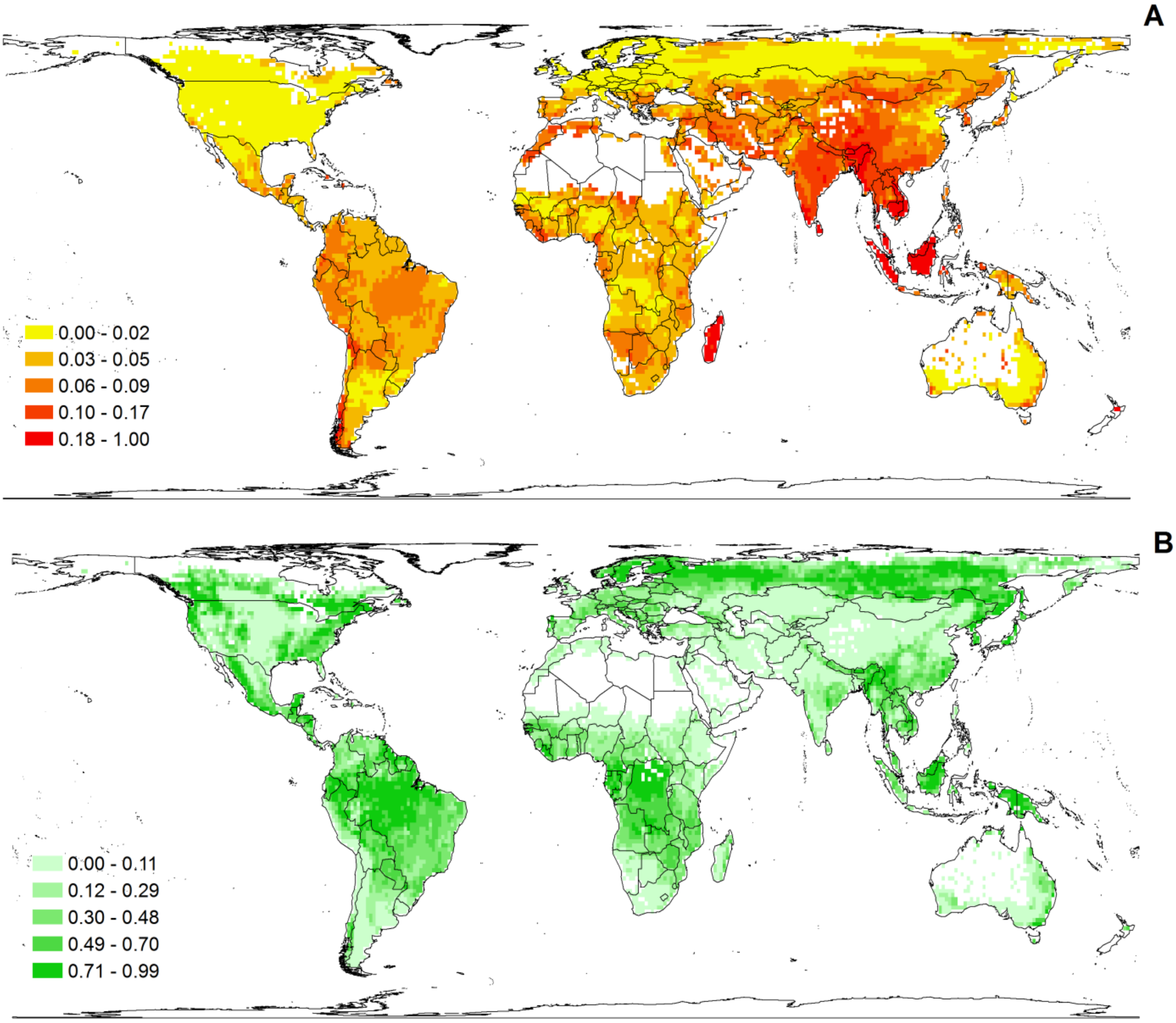


Figure S1.1. Proportion of threatened mammals (A) and proportion of forested area per grid-cell (tons/ha; B).

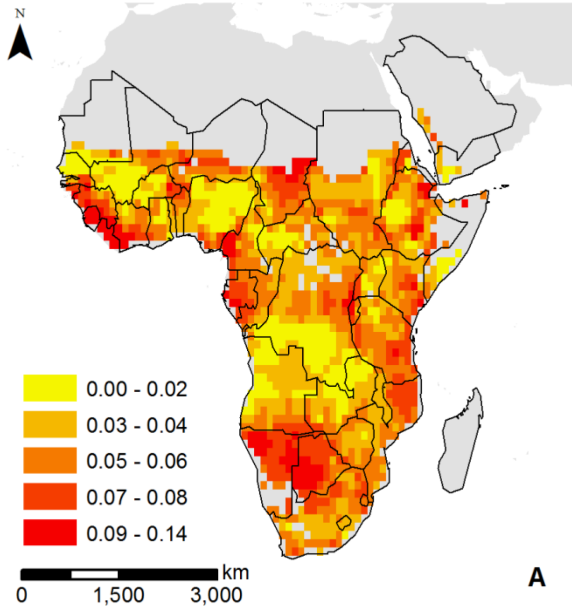


Figure S1.2. Proportion of threatened mammals (A) in the Afrotropics realm.

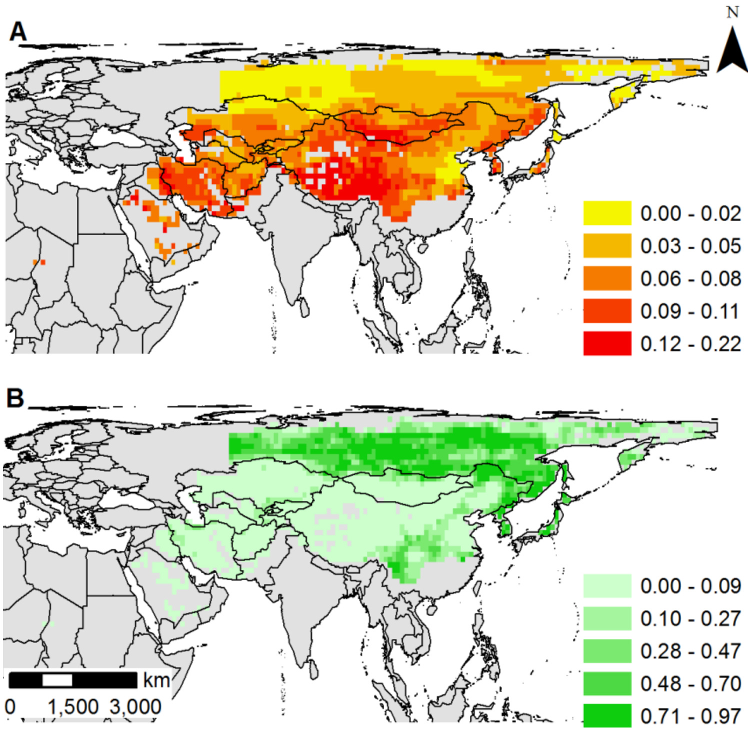


Figure S1.3. Proportion of threatened mammals (A) and proportion of forested area per grid-cell (B) in the Asia region (Palearctic realm).

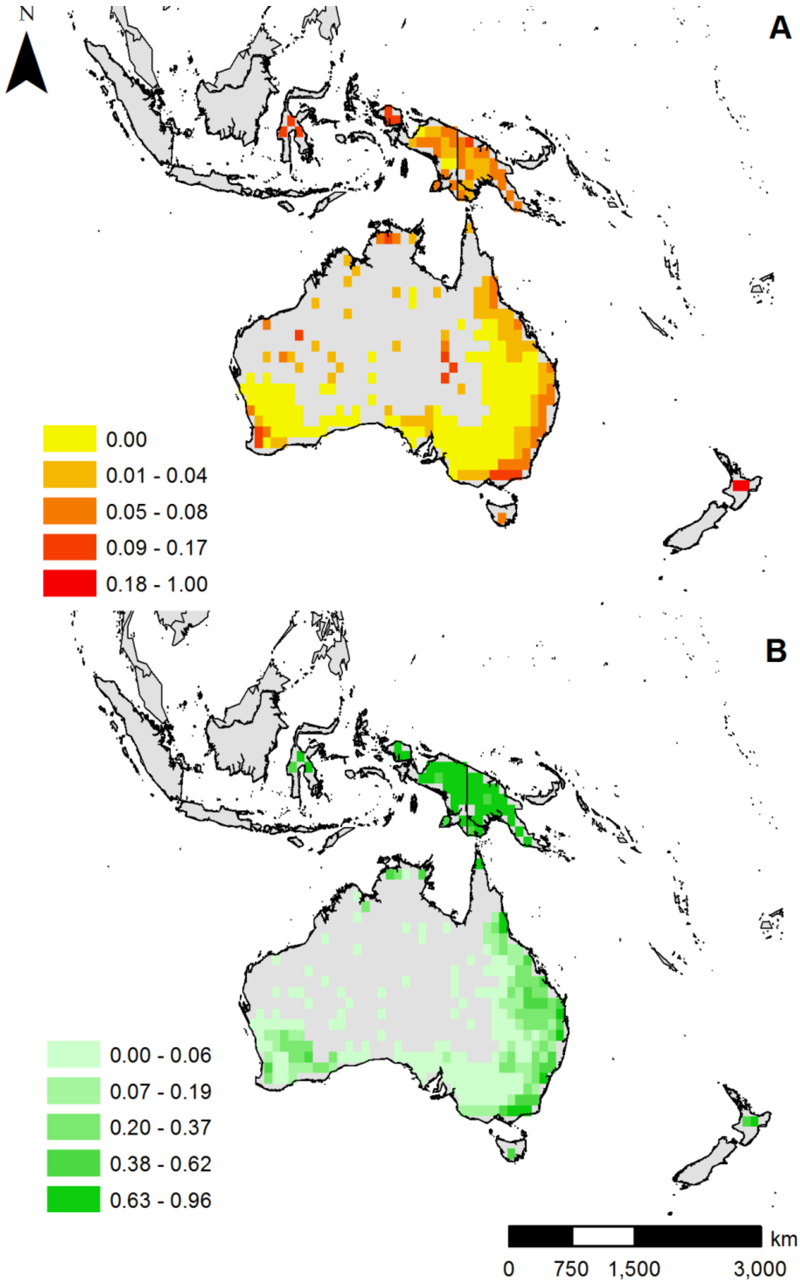


Figure S1.4. Proportion of threatened mammals (A) and forested area per grid-cell (B) in the Australasia realm.

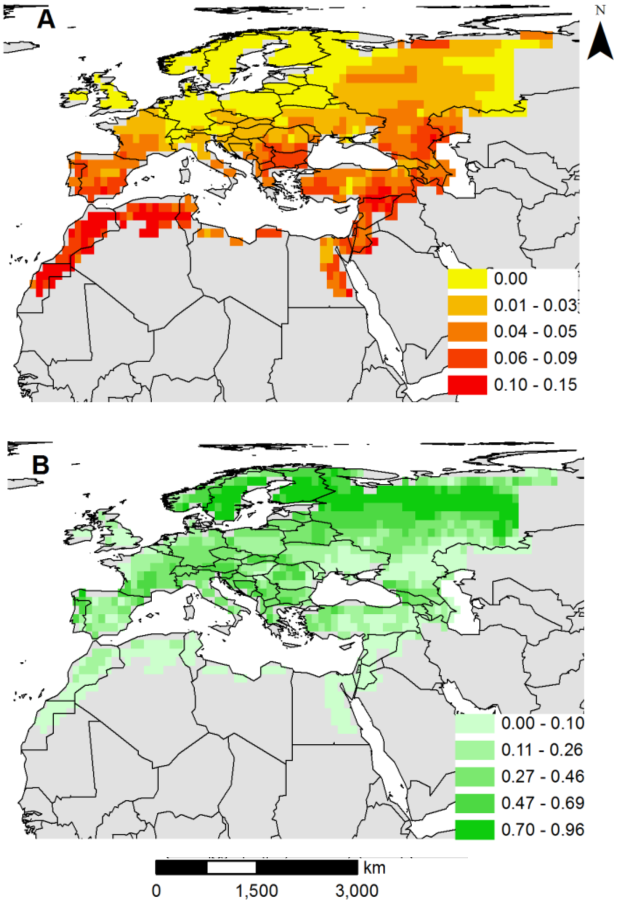


Figure S1.5. Proportion of threatened mammals (A) and proportion of forested area per grid-cell (B) in the Europe region (Palearctic realm).

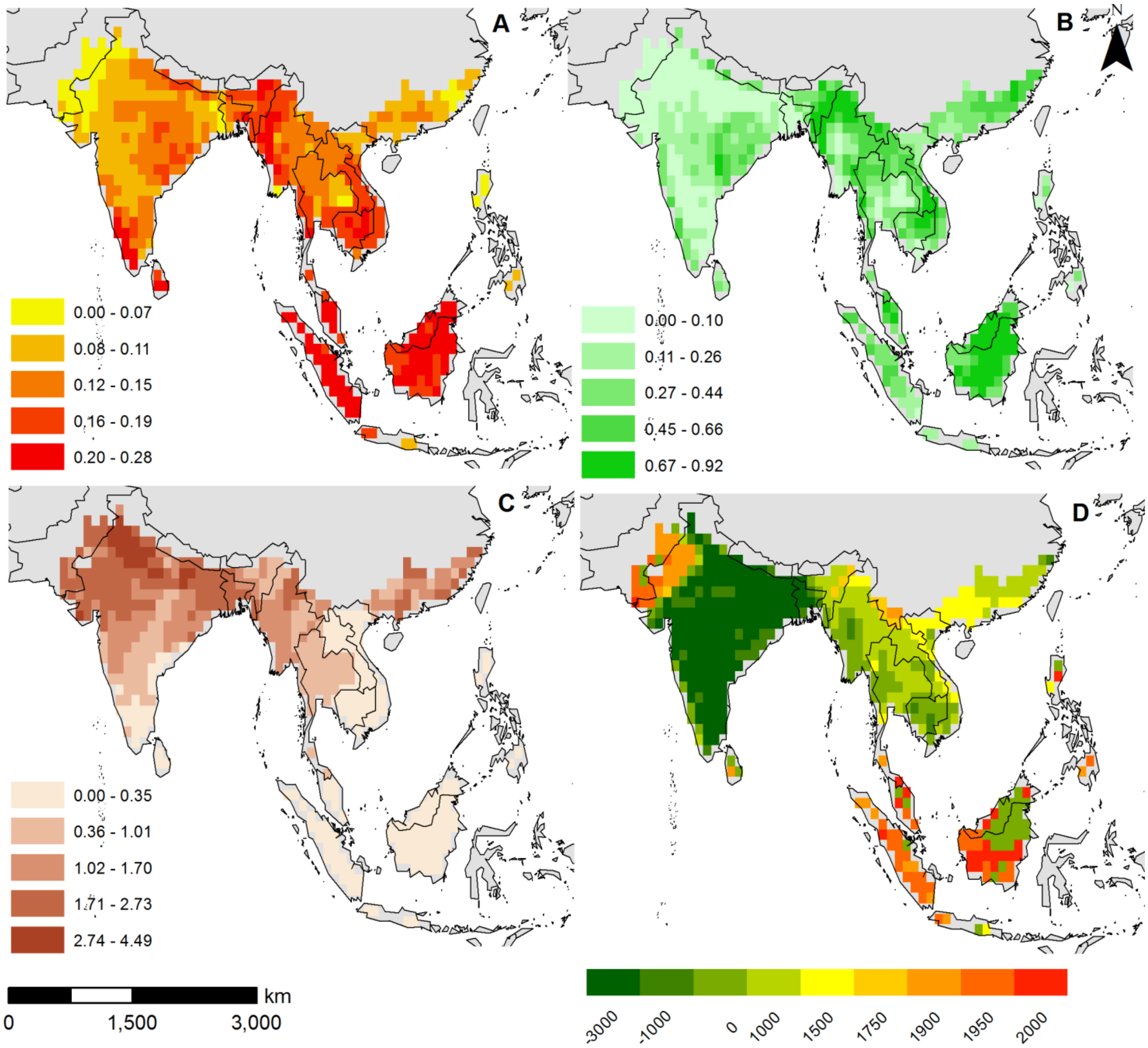


Figure S1.6. Proportion of threatened mammals (A), forested area (B), average wheat yields per grid-cell (tons/ha; C) and time of first use (D) in the Indomalay realm.

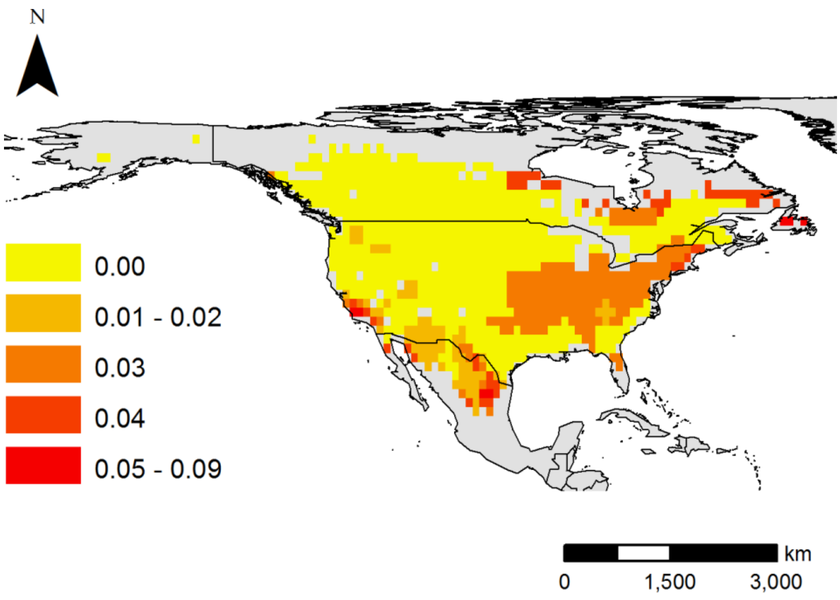


Figure S1.7. Proportion of threatened mammals in the Nearctic realm.

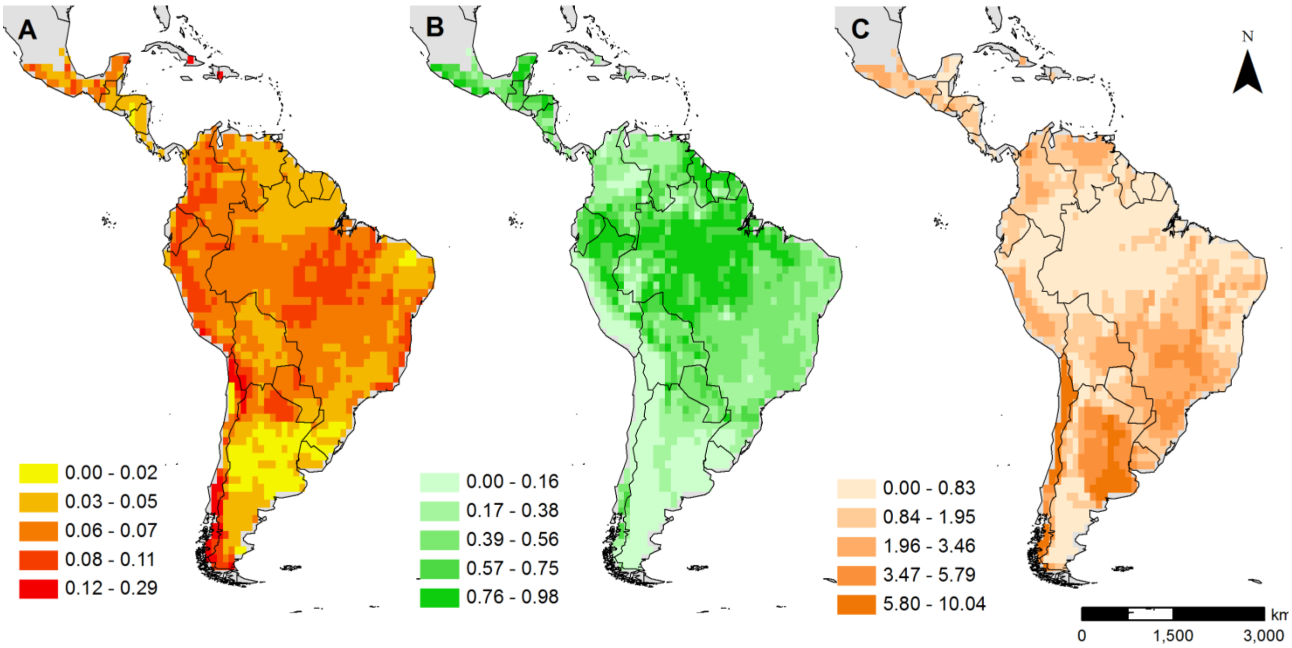


Figure S1.8. Proportion of threatened mammals (A), forested area per grid-cell (B) and maize yields (tons/ha; C) in the Neotropics realm.

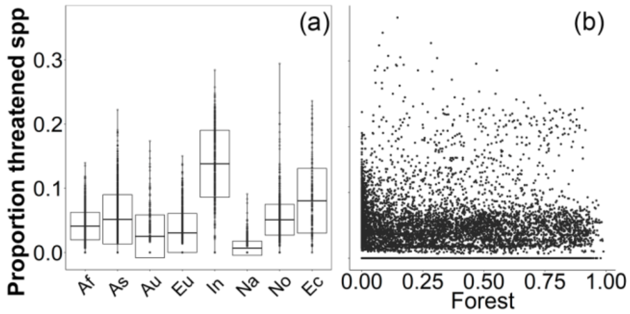


Figure S1.9. Boxplot and scatter plot showing the relationships between the relevant predictors in the global BRT model and the proportion of threatened species (raw data); (a) biogeographic realm (38.12% importance) and (b) forest extent (7.16% importance). *Afr* = Afrotropics; *As* = Asia; *Au* = Australasia; *Eu* = Europe; *In* = Indomalay; *Na* = Nearctic; *No* = Neotropics; *Ec* = Ecotone.

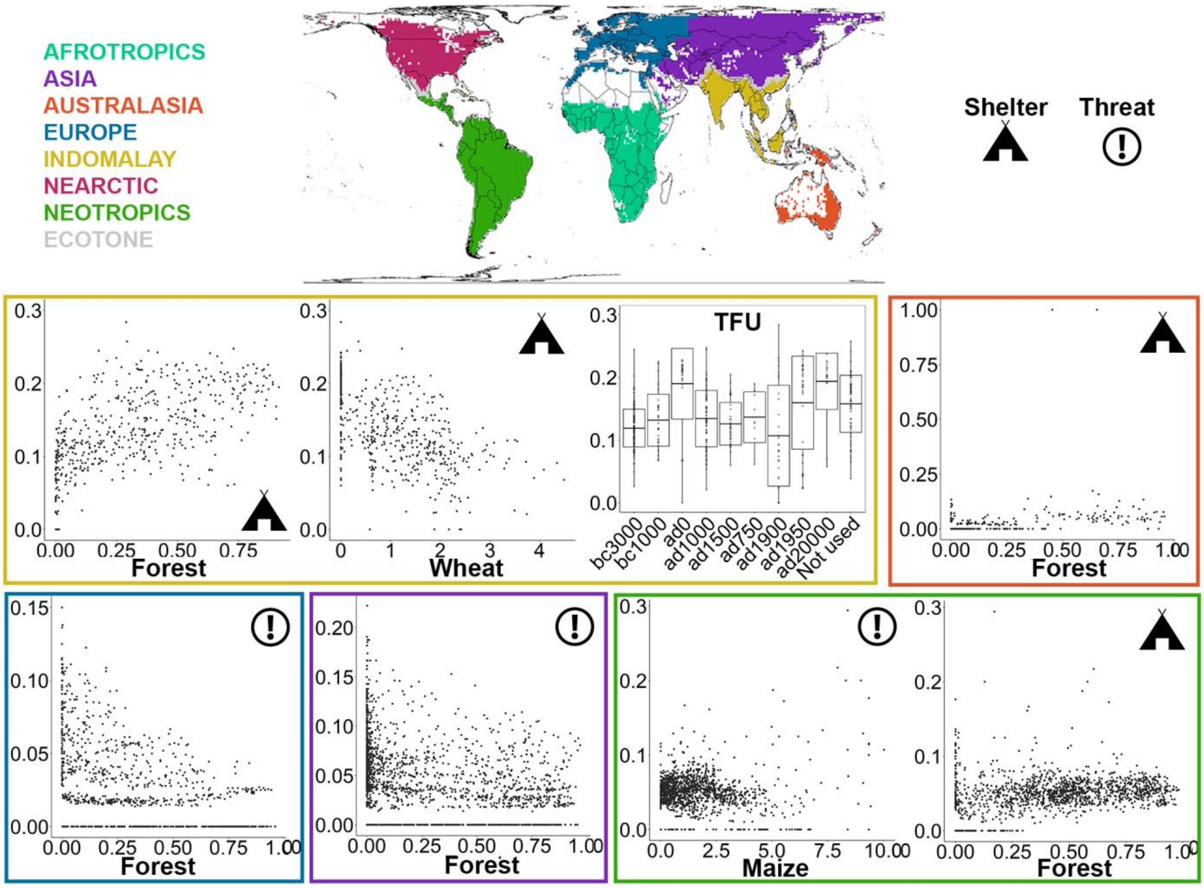


Figure S1.10. Scatter plots (continuous variables) and boxplot (categorical variable) showing the relationships between relevant predictors of the realms' BRTs and the proportion of threatened species (raw data). Colour legend matches realms' names, map and PDPs' borders. Y-axis in all plots represents observed proportion of threatened mammals. Symbols illustrate the hypothesis supported by each predictor (*threat* or *shelter). TFU* refers to the time period of first significant land use.

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Appendix S2. SUPPLEMENTARY RESULTS: BOOSTED REGRESSION TREES

Global:

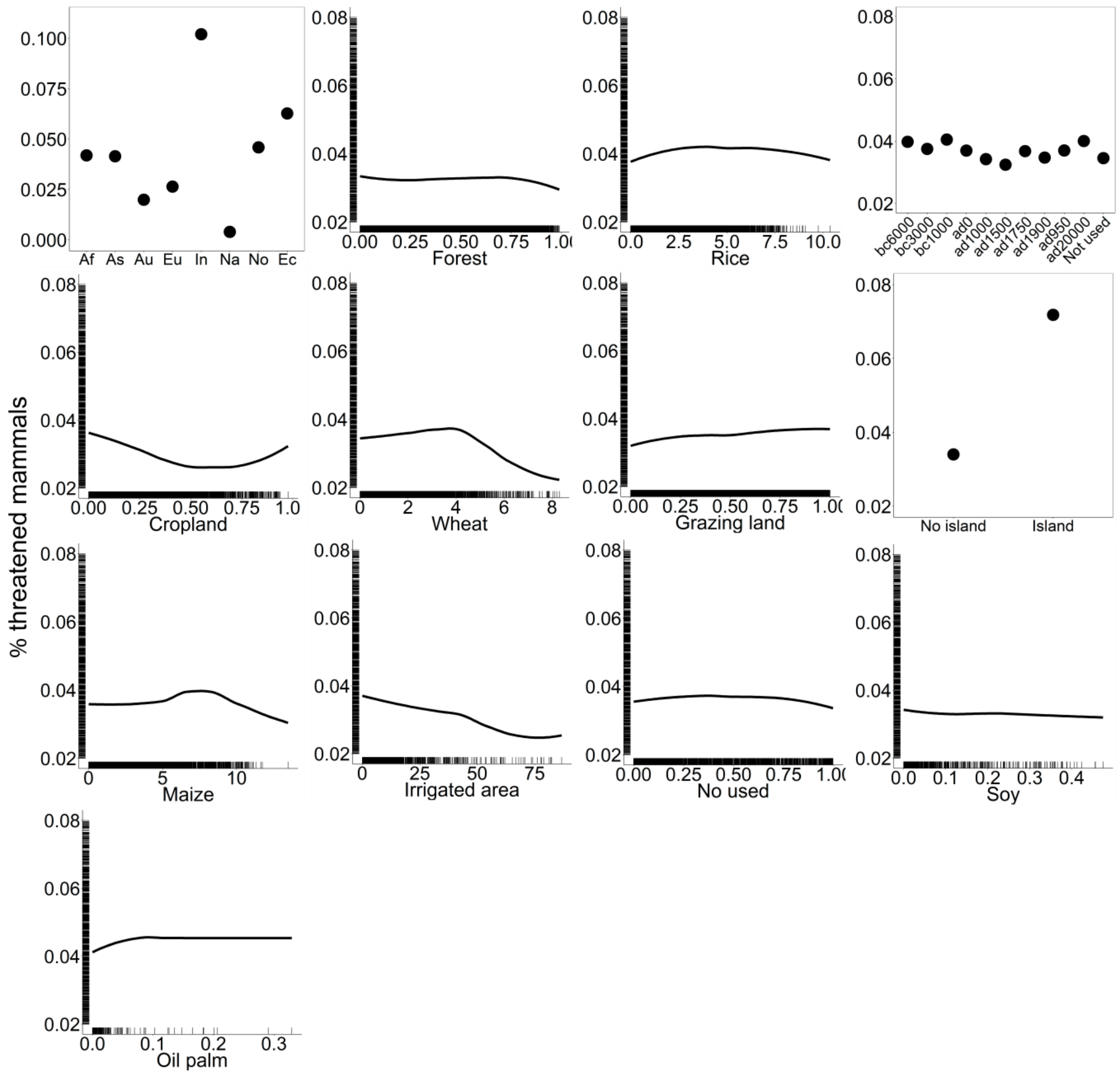

Figure S2.1. Partial dependence plots (PDPs) of all variables included in the Global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Afrotropics:

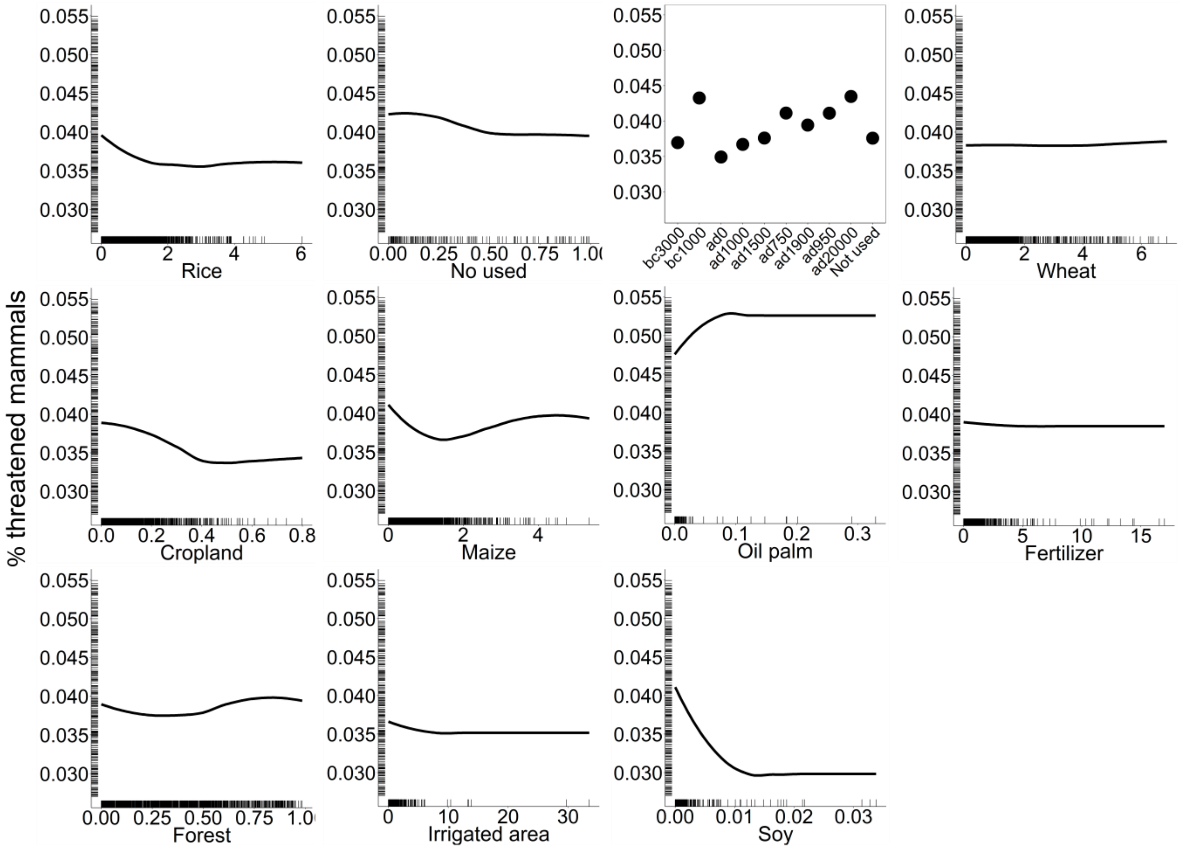

Figure S2.2. Partial dependence plots (PDPs) of all variables included in the Afrotropics BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).G

Asia (Palearctic):

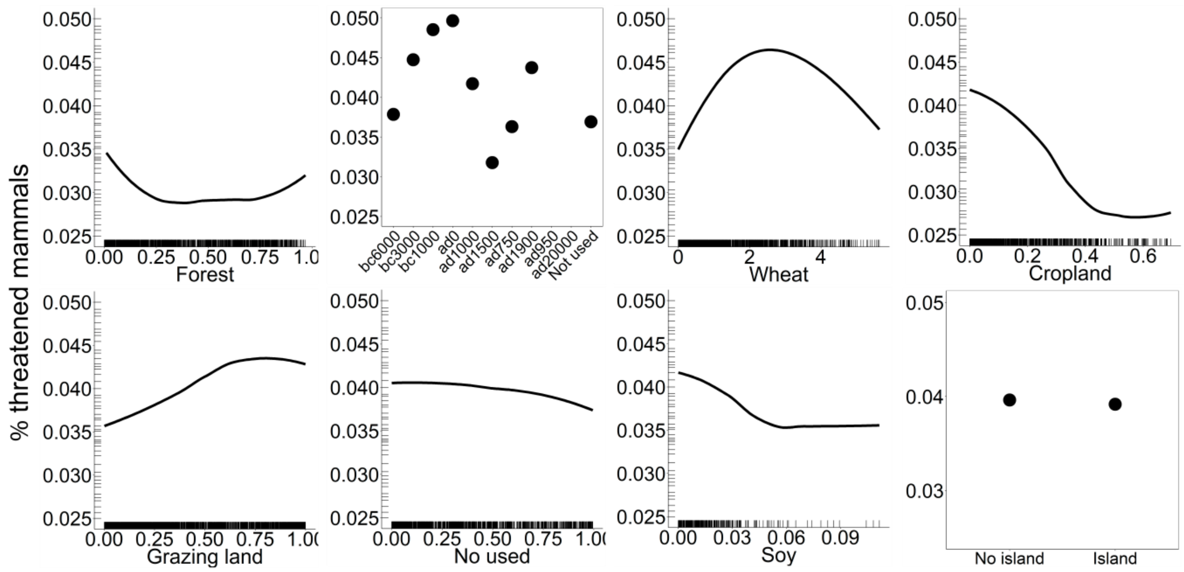

Figure S2.3. Partial dependence plots (PDPs) of all variables included in the Asia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Australasia:

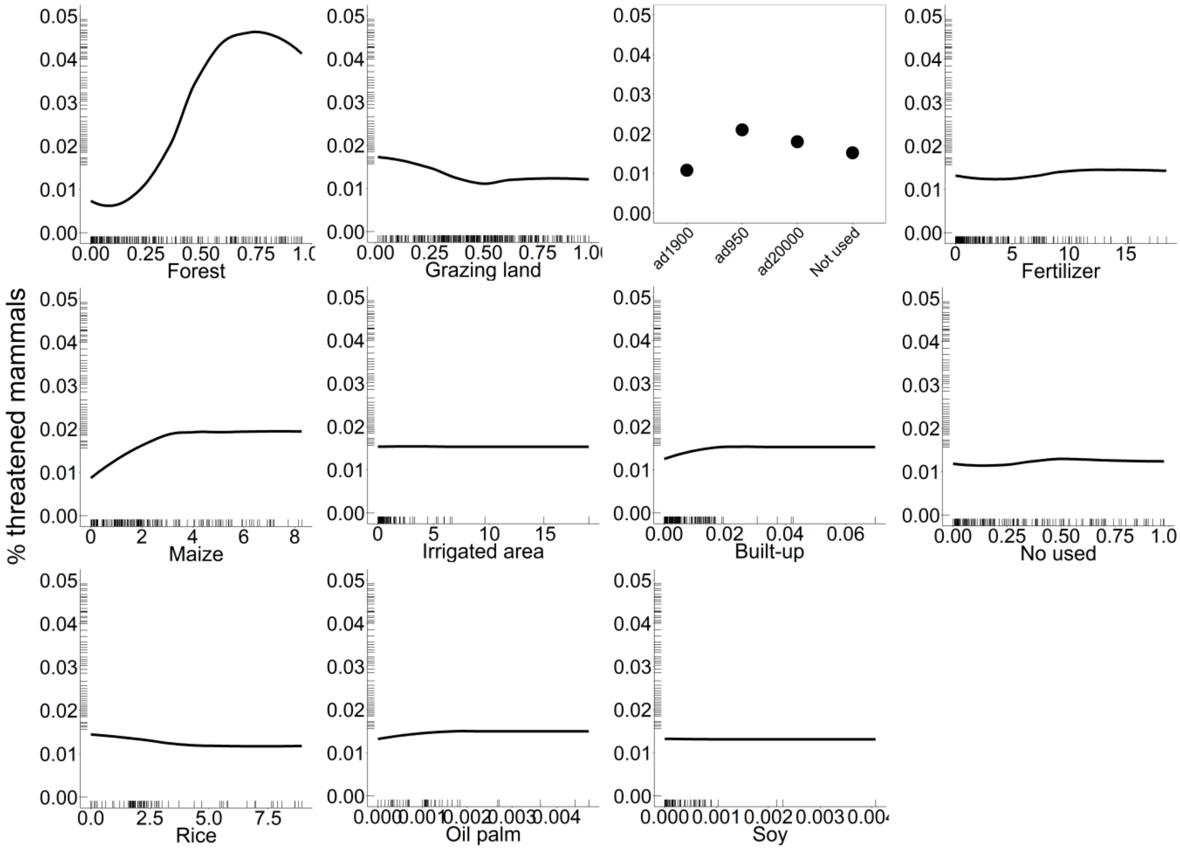

Figure S2.4. Partial dependence plots (PDPs) of all variables included in the Australasia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Europe (Palearctic):

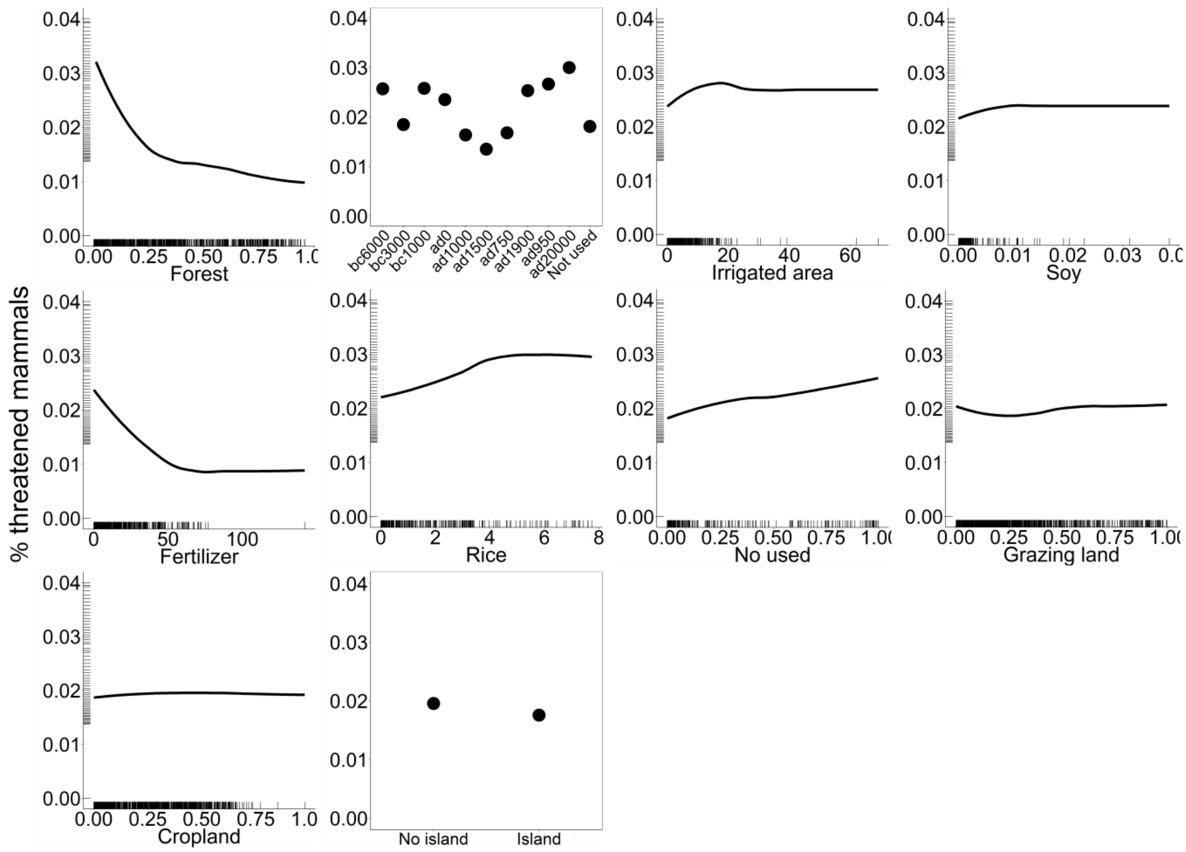

Figure S2.5. Partial dependence plots (PDPs) of all variables included in the Europe BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Indomalay:

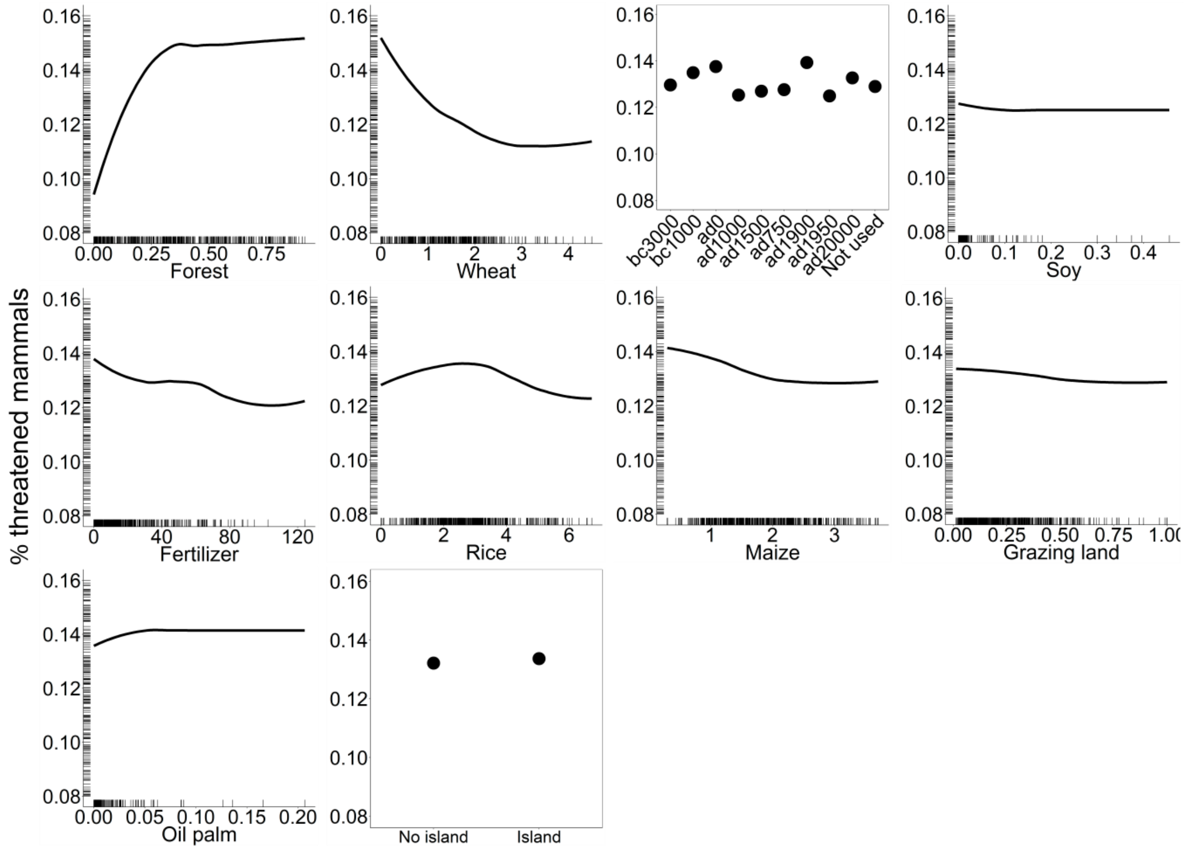

Figure S2.6. Partial dependence plots (PDPs) of all variables included in the Indomalay BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Nearctic:

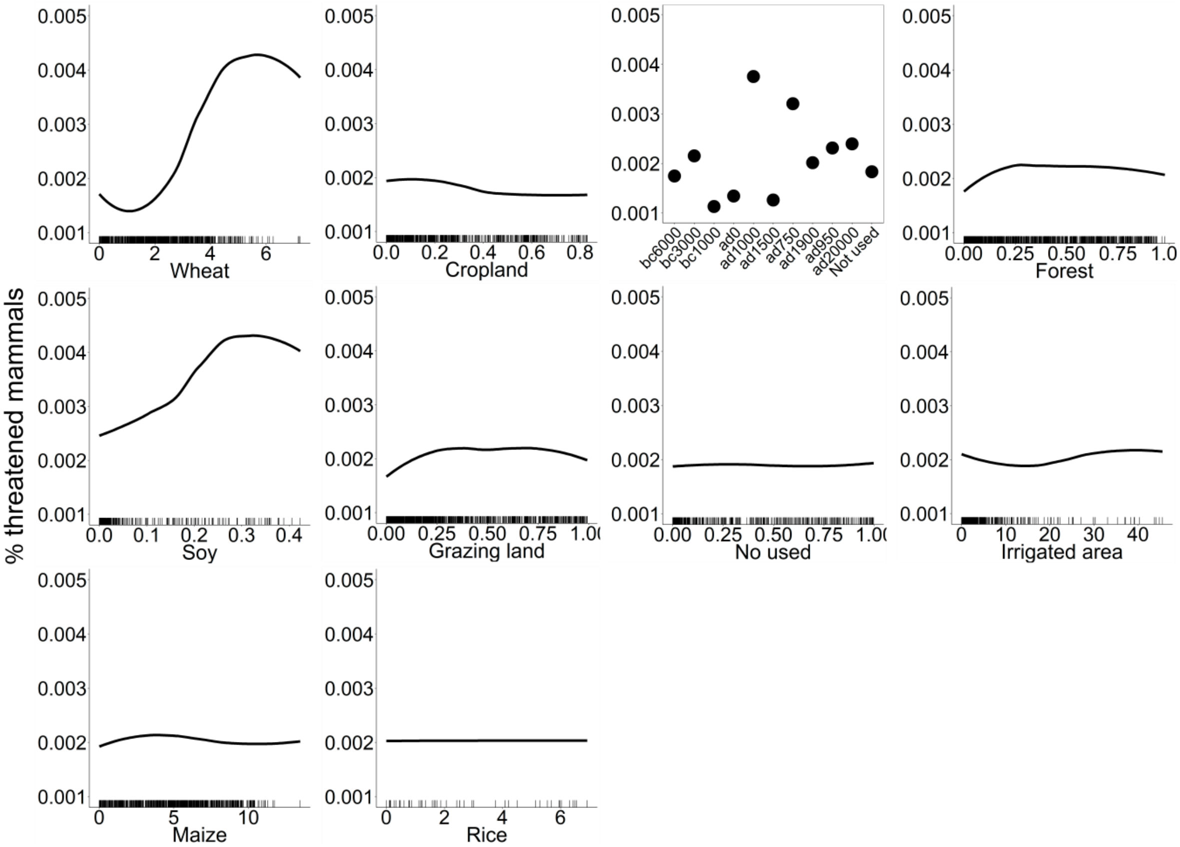

Figure S2.7. Partial dependence plots (PDPs) of all variables included in the Nearctic BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Neotropics:

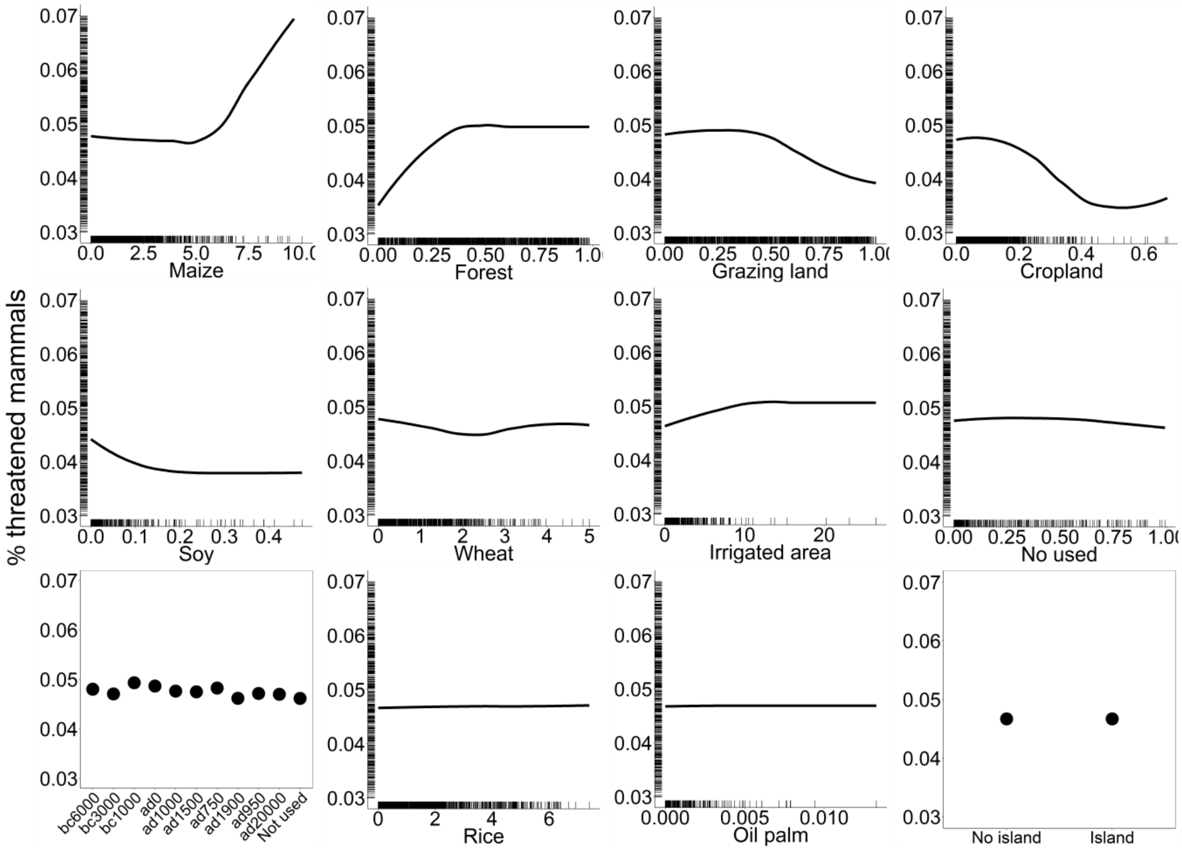

Figure S2.8. Partial dependence plots (PDPs) of all variables included in the global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

Table S2.1. Parameters and results of the BRTs, global and by realm, excluding the residual autocovariate (RAC). *Afro.* = Afrotropics; *Austr.* = Australasia; *Indo.* = Indomalay; *Neotrop.* = Neotropics. *Moran's I* was calculated for the residuals of each cell and the grid-cells surrounding it (all adjacent neighbours; max=8). *RAC,* residuals spatial autocovariate. Bold numbers indicate variables considered as relevant (i.e. their importance is greater than the expected under uniformity; thresholds are indicated in the last row).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
No. trees	1500	13500	8600	2700	7500	7700	6500	7900
Residuals Moran's I	0.37***	0.28***	0.52***	0.19***	0.33***	0.18***	0.32***	0.37***
% Deviance explained	71.71	48.04	56.68	33.6	68.1	71.14	36.15	43.55
Variables (importance, %)								
Land-use extent								
Built-up	~	~	~	7.22	~	~	~	~
Cropland	6.55	**10.7**	**12.65**	~	4.62	~	**18.18**	8.03
Forest	**10.71**	8.02	**29.77**	**39.15**	**26.24**	**29.13**	9.82	**18.29**
Grazing land	6.19	~	9.14	**11.86**	6.4	5.67	9.5	**11.12**
Not used	5.27	**9.86**	7.65	5.46	7.01	~	8.84	5.5
Land-use intensity								
Fertilizer	~	**9.65**	~	**11.94**	9.93	8.67	~	~
Irrigated area	4.53	6.4	~	8.1	**17.18**	~	8.73	7.05
Maize	4.25	**10.27**	~	4.61	~	5.24	8.76	**17.84**
Rice	6	**14.57**	~	2.09	5.24	5.79	0.34	3.77
Wheat	5.47	**11.4**	**13.74**	~	~	**14.66**	**14.49**	**9.3**
Oil palm	0.76	6.85	-	1	-	3.31	-	1.72
Soy	2.09	2.86	5.41	0.92	**10.33**	8.03	8.11	**10.92**
Land-use history								
Time of first use	6.81	**9.42**	**21.61**	7.66	**12.53**	**19.26**	**13.23**	6.46
Island	3.05	-	0.04	-	0.51	0.22	-	0
Realm	**38.33**	-	-	-	-	-	-	-
Relevance threshold	*7.69*	*9.09*	*12.5*	*9.09*	*10*	*10*	*10*	*8.33*

*** p<0.001, spatial autocorrelation exists; -, not existent/applicable; ~, variable excluded because its correlation with other/s one was ≥|0.7| (Spearman's ρ).

Table S2.2. Interactions table for the global BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	Realm	RAC
Cropland	0.00	0.01	0.01	0.00	0.03	0.02	0.00	0.00	0.00	0.01	0.04	0.00	0.01	0.02
Forest	0.00	0.00	0.00	0.02	0.00	0.01	0.02	0.02	0.00	0.00	0.02	0.16	0.17	0.04
Grazing land	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.05	0.04
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.05
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.02	0.01	0.01	0.01
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00	0.05	0.00	0.02	0.03
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.05	0.10
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.11	0.04	0.02
Oil palm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.04	0.74
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.69	1.11
Realm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.40
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.3. Interactions table for the Afrotropics BRT.

	Cropland	Forest	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Forest	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fertilizer	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oil palm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	Cropland	Forest	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.4. Interactions table for the Asia BRT.

	Cropland	Forest	Grazing land	Not used	Wheat yield	Soy	Time of 1st use	Island	RAC
Cropland	0.00	0.00	0.00	0.00	0.02	0.00	0.03	0.00	0.02
Forest	0.00	0.00	0.01	0.01	0.03	0.00	0.01	0.00	0.02
Grazing land	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.02
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.01	0.06	0.00	0.04
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.5. Interactions table for the Australasia BRT.

	Built-up	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
Built-up	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Forest	0.00	0.00	0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.02
Grazing land	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fertilizer	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oil palm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.6. Interactions table for the Europe BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Rice yield	Soy	Time of 1st use	Island	RAC
Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Forest	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.01	0.03	0.00	0.02
Grazing land	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01
Fertilizer	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.7. Interactions table for the Indomalay BRT.

	Forest	Grazing land	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	RAC
Forest	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.04	0.00	0.02
Grazing land	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fertilizer	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Oil palm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.8. Interactions table for the Nearctic BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Soy	Time of 1st use	Island	RAC
Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Forest	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Grazing land	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.07
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table S2.9. Interactions table for the Neotropics BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	RAC
Cropland	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.11
Forest	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.00	0.00	0.05
Grazing land	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
Not used	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Irrigated area	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Wheat yield	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
Maize yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.13
Rice yield	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Oil palm	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Soy	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Island	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00